UNIVERSITY COLLEGE OF WALES

ABERYSTWYTH

REPORT

OF THE

WELSH PLANT BREEDING STATION

FOR

1959

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Breeding for Resistance to Stem Eelworm in Oats
(*see page 33*)

WELSH PLANT BREEDING STATION
ABERYSTWYTH

REPORT

FOR

1959

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PREFACE

The work of the Welsh Plant Breeding Station has been published in numerous scientific journals, as well as in the Station's own bulletins and leaflets. In addition, three reports covering the periods 1919-1933, 1950-56 and 1956-58 have been published, and a full bibliography of publications up to 1955 is available as a separate volume.

The amount of data for publication is increasing rapidly, but owing to pressure on space in scientific journals there is often a considerable delay before fully documented papers can appear in print. Under these circumstances, it was considered desirable to issue an annual report from the Station.

This first Annual Report is not a guide to experiments, and no attempt has been made to cover all the work carried out at the Station during the year, especially because many of the experiments are of a long-term nature. As far as possible, therefore, emphasis has been given to research problems which are either nearing completion or where significant developments are expected in the immediate future.

The practical agriculturalist is primarily concerned with the fruits of research, and for this reason a modest attempt has been made to stimulate his interest in the significance of the work in progress. A number of short papers by individual members of staff are included in order to emphasise certain problems which are considered to be of topical or special interest.

I am extremely grateful to my colleagues for their ready collaboration in the preparation of this Report, and especially to Miss Irene D. Rees, for her most efficient editing and for seeing the publication through the press.

March, 1960 P. T. THOMAS.

STAFF

Director :	Professor P. T. Thomas, B.Sc., Ph.D.
Deputy Director :	Gwilym Evans, O.B.E., M.Sc.
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H. M. Roberts, B.Sc. (in charge of Seed Multiplication)
Joseph Lewis, B.Sc.
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Assistant : Miss Ceri F. Howells

Cytology : Keith Jones, B.Sc., Ph.D.
Christopher P. Carroll, B.Sc.

Assistants : Miss E. E. Davies, Miss Mair L. Jones, B.Sc.

Chemistry : G. ap Griffith, B.Sc., Ph.D.
Michael Hastings, B.Sc.

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Scientific Liaison Officer : Llywelyn Phillips, B.Sc.

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Farm Staff : HARRY JONES, Manager, Gogerddan and Frongoch
GLYNDWR PHILLIPS, Dip. Agric., Manager, Morfa Mawr Seed Multiplication Farm

THE WELSH PLANT BREEDING STATION

The Station was established in 1919 as a Research Department of the University College of Wales, Aberystwyth, by Sir R. George Stapledon, F.R.S., M.A., D.Sc., then Professor of Agricultural Botany. This development was made possible by the generosity of The Rt. Hon. Lord Milford, LL.D., who, in addition to providing a capital sum for the foundation of the Station, contributed annually for the first ten years towards its maintenance. The Station is now fully grant-aided by the Agricultural Research Council of England and Wales.

Sir R. George Stapledon, the first Director (1919-1942), was succeeded by T. J. Jenkin, C.B.E., D.Sc., (1942-1950), and followed by E. T. Jones, M.Sc., N.D.A., N.D.D. (1950-1958).

The present Director, Professor P. T. Thomas, B.Sc., Ph.D., also occupies the Chair of Agricultural Botany, and there is the closest possible liaison between the Station and the Department of Agricultural Botany.

DIRECTOR'S REPORT

Agricultural Research Council

It was my pleasure at the beginning of the first year as Director of the Welsh Plant Breeding Station to submit a memorandum to the Agricultural Research Council on the future policy of the Station, and to indicate the programme of research work envisaged during the next few years. This memorandum was fully discussed with the Council's Visiting Group which was composed of Professor K. Mather, C.B.E., F.R.S., D.Sc., (Chairman), Mr. David Lowe, C.B.E., Sir James Denby Roberts, J.P., Professor M. Skene, D.Sc., F.L.S., and Professor C. W. Wardlaw, Ph.D., D.Sc., M.Sc., F.R.S., together with Dr. E. E. Cheesman, Mr. G. G. Samuel, M.Sc., and Mr. P. A. C. Thorne. The Group's Report, approved by the Agricultural Research Council, provided very valuable advice and guidance, for which I am extremely grateful.

Developments in research

The organisation of research for plant breeding

In the breeding of herbage plants most of the attention has hitherto been given to total and seasonal productivity. While this aspect is of prime importance, the farmer is equally interested in the *value* of herbage for the production of meat, milk and wool. The future aim of the breeder should clearly be to develop improved varieties which are not only productive but also highly nutritious. At the same time he must ensure that these varieties possess a satisfactory mineral content and balance in relation to the needs of the healthy thriving animal.

An important consequence of this approach is that the plant breeder must no longer work in isolation, but should collaborate actively with other disciplines of which genetics, physiology and biochemistry are probably the most important at the breeding stage. For this reason, the Station is establishing a department of Developmental Genetics under Dr. J. P. Cooper, which aims at integrating genetics, physiology and biochemistry to satisfy the needs of the breeder. Mr. P. B. Vose will be primarily concerned with the basic physiology of herbage growth, and, in particular, with the mineral nutrition of crop plants.

Plant characters which are agronomically important are basically physiological and biochemical, their inheritance is complex and their expression is greatly influenced by the environment. Already we find considerable genetic variation in these characters, such as net assimilation rate, response to defoliation, carbohydrate content, various nitrogen constituents, and digestibility as measured by normal-acid fibre content. Useful response to selection has also been obtained for many of these characters, which is a first step towards the production of improved varieties.

Accumulation of nitrates in herbage

The importance of paying attention to the mineral content of herbage is well illustrated by the work of Dr. ap Griffith, who has demonstrated the accumulation of abnormally high levels of nitrate nitrogen in a wide variety of herbage crops. These have included most of the important grass species, oats for grazing, forage kales and rape. In some instances, he has also been able to specify the conditions under which these accumulations are likely to occur.

The work is significant in at least three directions, of which the first, and most important, is that nitrate is a well-known toxic principle which may be associated with adverse effects on the growth and performance of animals. While no experiments on the feeding of nitrate-rich herbage appear so far to have been undertaken in this country, our attention has already been drawn to instances of serious digestive upsets in animals, particularly when there has been an abrupt change to feeding this kind of herbage. It seems likely that these findings will relate not so much to loss of animals, but to the problem of sub-optimal growth and reduction in milk yield, especially in the autumn, or after a check in growth of herbage in mid-summer.

The second implication of Dr. ap Griffith's work will interest the plant breeder in that grass species, and even genotypes, have been found to differ in the degree of nitrate accumulation, so that attention can be given to the production of new varieties with increased efficiency for the utilisation of nitrogenous fertilisers.

External factors such as plant spacing, light intensity and temperature, however, have a profound influence on the degree of nitrate accumulation, sometimes even to the point of masking inherent differences between varieties. Thus one can deduce from the

results already available that nitrate accumulation is less likely in a high-density sward (such as good permanent grass) than in a low-density open sward too often typical of a young ley. This conclusion emphasises the superiority of high-tillering grass varieties, and possibly may also lead us to consider a somewhat higher seed rate for the rapid establishment of a high-density sward which would respond to heavy application of fertilisers without undesirable 'luxury' uptake of nitrates in the herbage.

Hill pasture improvement

Mr. Iorwerth Jones has briefly summarised some of the work carried out at Aberystwyth over a number of years on hill pasture improvement (p. 45). Many of the principles developed from this work have been applied successfully on a practical scale in Wales and elsewhere. It is clear, however, that the choice of method largely depends on the degree of improvement desirable, or which could be reasonably expected under a particular set of conditions. Naturally, many problems remain to be solved, but their importance can now be assessed in relation to further research work on the improvement of hill pastures.

Probably the greatest need is to introduce a vigorous legume. To this end, work has commenced on the problem of effective nodulation in white clover in conjunction with the breeding of productive varieties adapted for hill land. Under relatively acid and low fertility conditions on the hills, it is also important to produce varieties which are minerally efficient, and Mr. Vose's work (p. 18) has shown that there are significant genotypic differences both in the requirements and uptake of minerals such as calcium.

Persistency and ease of establishment under relatively adverse conditions are two important agronomic characters for improved grasses on the hills. Among a number of grass species and varieties which have been sown on upland areas, certain genotypes (particularly from varieties such as S.23 perennial ryegrass) have persisted for as long as 15 to 20 years. These form a natural source of material which has already been screened for persistency, and will be utilised for breeding purposes.

In order to study the establishment, persistency and productivity of different species and varieties, seven small hill areas near Aberystwyth are being subjected to different cultural treatments,

some of which also involve the use of chemical herbicides. These areas have been chosen to represent different hill associations where the dominant plants are *Agrostis*, *Agrostis*/fescue, *Nardus*/fescue, *Nardus*, *Molinia*, heather or *Scirpus*.

Breeding for disease resistance

The importance of breeding for resistance to disease is well illustrated by the work of Dr. D. J. Griffiths and his colleagues on cereals and *Brassicae* crops. Resistance to mildew, crown rust and stem eelworm has been successfully incorporated into a single variety in the spring oat Manod, representing the first variety released to British agriculture which is resistant to all three diseases.

Good progress has also been made in the development of an adapted variety of rape resistant to clubroot disease, and a promising series of progenies from a wide range of crossing combinations of *B. oleracea* is now being tested under both lowland and upland conditions.

Genotypic differences in reaction to chemical sprays

The discovery by Mr. J. D. Hayes of a single gene which controls resistance or susceptibility of varieties of barley to DDT has several implications. In the first place, it has provided a means whereby the purity of varietal stocks can be quickly assessed, and the technique is now being adopted at several seed testing stations.

Secondly, this work leads to the possibility of breeding varieties of crop plants resistant to damage by protective chemicals used in agriculture. Dr. Cooper (p. 16) has already started selecting for tolerance to a higher concentration of Dalapon in *Dactylis* and *Lolium*, the object being to develop more effective control of gramineous weeds in crops grown for seed.

Other activities

Staff

We wish to congratulate Mr. Gwilym Evans, M.Sc., on being awarded the O.B.E., by Her Majesty The Queen in January 1959. For the past 30 years, Mr. Gwilym Evans has been responsible for the development of seed production and the authentication of pedigree grasses and clovers, and he has made an outstanding contribution to the scientific work of the Station.

We extend our best wishes to Mr. J. O. Parry-Williams, M.B.E., who retired on 30 September 1959, after 50 years of loyal service to the College, 40 of which have been as Secretary and Establishment Officer of the Welsh Plant Breeding Station. His successor is Mr. James Wilson Ellis, D.P.A., A.C.I.S.

The following resignations took place: Dr. D. Gareth Rowlands to take up an appointment with Unilever Ltd., Mr. J. R. F. Piette, L. és S. to the Welsh Department, University College of Wales, Aberystwyth, and Mr. Michael Hastings, B.Sc., to N.A.A.S. Mr. W. E. J. Milton, M.Sc., N.D.A., also left at the end of the year.

Mr. D. Gareth Jones, B.Sc., was appointed Microbiologist.

The following members of staff visited research institutions in Europe with the aid of travel grants from the Agricultural Research Council:

Dr. J. P. Cooper and Dr. E. L. Breese, jointly to visit France, Belgium, N.W. Germany, Denmark, Sweden and Norway.

Mr. J. D. Hayes, to visit Holland, Denmark and Sweden.

Mr. Joseph Lewis to attend the 12th International Seed Testing Congress in Oslo. He also visited research centres in Sweden and the Netherlands.

At the invitation of the Secretary, European Association for Research in Plant Breeding, Mr. A. R. Beddows attended the Second Eucarpia Conference at Cologne, 6-8 July 1959, and joined the post-congress tour of research institutions, namely, (i) Max-Planck-Institut für Züchtungsforschung, Köln-Vogelsang and Rosenhof; (ii) Landwirtschaftliche Hochschule, Hohenheim, and (iii) Bayerische Landessaatzuchtanstalt, Weihenstephan bei Freising. Visits were subsequently made to Reckenholz, a sub-station of Versuchsanstalt Zürich-Oerlikon, Switzerland, and to the Station Centrale de Genetique, Versailles, Ecole Nationale d'Agriculture de Grignon and Établissements Vilmorin-Andrieux, Verrières.

Mr. P. B. Vose returned to the Station in January 1959, after one year in the Dep. Agronomy, University of California, U.S.A.

Dr. A. Troughton resumed his work in August 1959, after one year in New Zealand as the result of an award of a New Zealand National Research Fellowship tenable at Palmerston North.

Dr. Keith Jones, who had received a National Research Council Post-doctorate Fellowship tenable in the Canada Department of Agriculture, Ottawa, for 12 months to work on cytotaxonomy of Canadian grasses, came back in September 1959. On his way home he was enabled by a grant from the Agricultural Research Council to attend the 9th International Botanical Congress in Montreal.

Visiting Research Workers

Dr. L. Dessureaux, Ministère de l'Agriculture, Station Expérimentale, Ste. Anne de la Pocatière, Quebec, Canada, returned to Canada in February 1959, after spending 16 months at the Station studying 'The inheritance of tolerance to manganese toxicity in lucerne.'

Mr. Claude D. C. Pfitzenmeyer, a British Council Scholar from Paris, completed his studies on 'The autecology of *Arrhenatherum elatius* (L.) J. & C. Presl and its intergeneric relationships' for which he was awarded the degree of M.Sc., Univ. Wales.

Mr. J. Sithamparanatham, a British Council Scholar from Ceylon, commenced his research work on 'Agronomic studies on Yorkshire fog for hill land' at the commencement of the session, with a view to presenting a thesis for the degree of Ph.D., Univ. Wales.

Mr. M. A. Baluch, West Pakistan Department of Agriculture, Tandojam, who holds a Colombo Plan Fellowship (administered in U.K. by British Council) arrived in September 1959, for advanced post-graduate training in plant breeding techniques prior to continuing his studies in Uganda.

Mr. K. Ahmed, Pakistan Central Jute Committee, Dacca, also a recipient of a Colombo Plan Fellowship, commenced a period of advanced post-graduate training in plant breeding in Sept. 1959.

Post-graduate students

Mr. W. I. J. Davies, who held a University Studentship, University College of Wales, Aberystwyth, completed his research work, and is preparing a thesis on 'The influence on the performance of certain species and strains of herbage grasses of (a) low and high fertility; (*b*) low and high altitude and (*c*) spaced plants, drills and swards' in submission for the degree of M.Sc., Univ. Wales.

Mr. K. J. R. Edwards, Univ. Reading, an A.R.C. Research Scholar, commenced research work on 'Leaf development in rye-grass' in October 1958.

Mr. L. Beevers, Univ. Durham, was awarded a special A.R.C. grant to work in the Department of Agricultural Botany, U.C.W., on 'The biochemical assessment of different genotypes of herbage grasses in relation to their physiological characters,' which he started in October 1958.

Visitors

During the year, the Station had a total of well over 2,000 visitors made up of organised parties and individuals from home and overseas. Amongst the countries represented were Australia, Canada, Ceylon, Denmark, Eire, Ethiopia, France, Germany, Holland, India, Iran, Israel, Japan, Kenya, Korea, New Zealand, Nigeria, Northern Rhodesia, Pakistan, Poland, Portugal, Rhodesia and Nyasaland, South Africa, Sudan, Sweden, Thailand, Turkey, Uganda, Uruguay, U.S.A., U.S.S.R., West Indies.

In addition the following special groups met at the Station:

The Grassland Committee of the Scottish Agricultural Improvement Council.

The Aberystwyth Seeds Committee of the N.I.A.B.

Welsh Seed Growers Federation: Field Day at Morfa Mawr attended by 170 persons.

Meeting to discuss herbage virus diseases and inspect the plots at the Station at which representatives were present from the A.R.C., N.A.A.S., Rothamsted Experimental Station, the Pathological Laboratory at Harpenden, and East Malling Research Station.

The Jubilee of the Cardiganshire Antiquarian Society was celebrated by a meeting at Plas Gogerddan which 96 members attended.

Conferences and Lectures

Members of staff read papers before the Genetical Society at its meetings in London, Birmingham and Dundee, and continued to lecture to the Honours Botany and Agricultural Botany students, U.C.W., Aberystwyth.

The usual Herbage Seed Crop Inspectors' Course for Trainees and the Refresher Course for Cereal Seed Crop Inspectors were held at

the Station, at both of which members of staff gave lectures and demonstrations.

There was a joint discussion on population genetics held in the Department of Agricultural Botany, U.C.N.W., Bangor, which some members of staff attended.

A joint Symposium between members of the Welsh Plant Breeding Station and the Grassland Research Institute was held at Hurley in September 1959, at which I gave the opening address on 'The integration of research on grass.' Members of both staffs also read papers on problems of mutual interest.

A weekly Staff Discussion Group has been organised at the Station at which problems connected with the work in progress are discussed. At one of these meetings, Mr. W. F. Raymond, Grassland Research Institute, Hurley, gave a talk on 'Some factors affecting the digestibility and nutritive value of herbage.'

Acknowledgements

It is a pleasure to record our thanks to The Rt. Hon. Lord Milford, LL.D., for his generous donation towards establishing a film unit at the Station.

We are grateful to numerous firms, organisations and individuals for the supply of seeds, plants, chemicals and insecticides for experimental purposes.

We also wish to thank the National Agricultural Advisory Service, National Institute of Agricultural Botany, Forestry Commission, the Grassland Research Institute, the Hill Farming Research Organisation, the Royal Botanic Gardens, Kew, and the staff of the Institute of Rural Science, Aberystwyth, for helpful collaboration.

In addition we wish to thank the following who have generously provided land for special experiments : Capt. G. L. Bennett Evans, O.B.E., Manod, Llangurig ; Mr. D. Davies, Llety Ifan Hen, Bontgoch ; Mr. Gregory, Bryn-y-Pys Home Farm, Overton ; Mr. M. Morgan, Tynrhyd, Devil's Bridge ; Mr. F. W. Rogers, Bacheldre, Churchstoke ; Mr. H. E. Williams, Bwlch-crwys, Devil's Bridge.

DEVELOPMENTAL GENETICS

J. P. Cooper

The aims of the research programme are to study the genetic and physiological basis of agronomic differences in the herbage grasses and legumes, and to develop selection techniques which can be used by the plant breeder. In the past year attention has been concentrated on genetic differences in leaf and tiller development, in carbohydrate and nitrogen metabolism, and in the uptake and utilisation of minerals, especially calcium.

GENETICS

Genetics of production characters (J.P.C., K.J.R.E.)

The study of the heritability and response to selection of production characters in ryegrass has been extended to leaf size and rate of leaf appearance, since the growth analysis of several ryegrass varieties has shown that differences in yield are based largely on differences in leaf area.

The heritability of these characters has been estimated from parent/progeny correlation and from the analysis of variance of full-sib families (see p.71). The two methods of estimation agree well and provide a useful indication of short-term response to selection. Some additive genetic variation for both characters exists within varieties, and rapid response to selection can occur.

These changes in leaf size are based on differences in cell size and number. Leaf width is determined largely by the number of cell rows, but leaf length is influenced by cell length also.

Selection for leaf size or rate of leaf appearance independently has no regular effect on dry matter yield, largely because of a negative correlated response between these two characters. Selection for total leaf area has therefore been started.

In the selection experiment for date of ear emergence in Irish and Kent ryegrass, response has continued in the fifth generation; the range obtained from Irish is 61 days and from Kent 88 days, compared to 20 and 17 days respectively in the original populations. Ample genetic variation still exists within the selection lines. Low fertility continues in some lines and has decreased the possible selection differential. This experiment has been extended to compare the release of variation from inter-population crosses with that from crosses within populations.

Simulated sward selection (J.P.C., K.J.R.E.)

The genetic control of dry matter production under controlled competition and defoliation has been studied directly, using a simulated sward technique. Varietal differences in tiller number, dry weight/tiller and dry weight/plant could be detected, although these differences were influenced by the level of cutting ; the pasture varieties (Kent, S.23) produced relatively more than the hay varieties under close cutting.

Encouragingly high estimates of heritability have been obtained for tiller number, dry weight/tiller and dry weight/plant in Italian, Irish and Hunsballe ryegrass, but there was again a pronounced interaction between family performance and level of cutting :

Estimates of heritability for production characters in a simulated sward, calculated from the analysis of variance of full-sib families.

	Italian	*Irish*	*Hunsballe*
Tiller number	0.43	0.79	0.56
Dry weight/tiller	0.67	0.27	0.51
Dry weight/plant	0.57	0.46	0.28

Biochemical variation (J.P.C., L.B., M.A.F.)

Standard techniques have been developed for the analysis of carbohydrate and nitrogen fractions in individual genotypes of ryegrass, and also for the chromatographic assay of particular amino-acids and organic acids. Quantitative differences in all these components have been found between 4 genotypes of perennial ryegrass, two each from S.24 and S.23, there being a twofold range in total carbohydrate content between the lowest and highest genotypes. The next step is an estimation of the heritability of this biochemical variation and its response to selection.

The degree of resistance to Dalapon (2.2 dichloropropionic acid) has been tested in several varieties of cocksfoot (Danish, Brage, S.37, S.143) in both the seedling and mature plant stage. No varietal differences in susceptibility could be detected, but a few resistant plants occurred in all varieties. Further selection for resistance is in progress in both cocksfoot and ryegrass.

Genetic variation exists within ryegrass varieties for all characters which have been investigated, including anatomical and

biochemical differences, and useful response to selection should be possible. The major problem is to decide which of the many morphological and physiological characters are important in determining yield and nutritive value under sward conditions.

PLANT PHYSIOLOGY (P. B. Vose)

The physiology of the vegetative grass plant (P.B.V.)

Most of our knowledge on the growth and nutritional physiology of the grass plant is related to the flowering plant rather than to vegetative material. Accordingly, it was decided to obtain basic information on the growth pattern, composition and mineral uptake of the vegetative plant, and in addition to obtain data which should assist the planning of rational field experiments, when seed of non-flowering material becomes available.

Vegetative perennial ryegrass S.101 has been grown in solution culture at three levels of nitrogen. Two cutting treatments, frequent and infrequent, were superimposed. It was found that in the 1N (84 p.p.m. N.) series the tiller number continued to rise throughout the 6 months' growing period; there was a definite cutting effect, the tiller number rising much higher in the infrequent than in the frequent series. At both the 1/5N (16.8 p.p.m. N.) and 1/20N (4.2 p.p.m. N) levels tiller numbers reached a peak between the twelfth and thirteenth weeks. In the 1/5N series the number remained steady until the end of the season, while the 1/20N series showed a progressive decline due to the die-back of older tillers. No new ones were produced.

Fructosan, the main storage product in perennial ryegrass, reached peak amounts fairly early in the season, thereafter declining with further leaf growth and the increased number of cuttings. Fructosan was inversely related to nitrogen treatment and protein content, the 1N series having very much less than either 1/5N or 1/20N. The roots in particular showed very big differences at the conclusion of the experiment, those on 1N having negligible amounts of reserve carbohydrates. In the 1N and 1/20N series little cutting effect was observed, but in the 1/5N series a quite distinct effect was apparent. There appeared to be little difference in sucrose content with either nitrogen level or cutting, but hexoses followed the pattern of fructosan, although the differences were not so marked.

The final root weights reflected the fructosan trends. The roots of the 1/20N and 1/5N series remained white and healthy, while those of the 1N plants became brown and limp, and the root cell-wall

structure was visibly sloughed off. The 1N plants had the lowest root weights, while the frequently cut series weighed slightly less than the plants cut infrequently. Apparently the high N stimulation of the foliage had drained all reserve carbohydrates from the roots.

The high nitrogen gave high foliage yields with very low soluble carbohydrate content, low root reserves and there was actual breakdown of roots. Increased cutting exaggerated this. Lower nitrogen levels gave increased carbohydrates and root reserves but at the expense of lower yield, with much lower tillering and protein. The results in solution culture probably exaggerate the condition as it would be in the field, although the trend will be the same. It follows, therefore, that in the field a system of management must be adopted to ensure that protein and yield are kept at a satisfactory level without causing very low carbohydrate levels and very low winter root reserves.

Intraspecific differences in nutrient uptake and assimilation (P.B.V.)

As crop yields are approaching a ceiling more detailed attention to the components of yield is required; although factors such as net assimilation rate have received widespread attention, the concept of selecting plants according to nutrient uptake and assimilation is relatively new. The general aim of the work at present is to uncover as much potential nutritional variability as possible in *Lolium* and *Trifolium*, with the more specific aim of selecting plants which may be better adapted to growing under hill conditions on soils of low pH and of low calcium and phosphate status. As so little work has been done on the general subject it is necessary to devise techniques for selection from scratch, this being complicated by the fact that the variations will be relatively small, that only 1 in 1000 plants will be of real value in a breeding programme and large numbers must be handled, while the methods adopted must be non-specialist in nature and such that the breeder can use them easily.

An experiment to investigate the resistance of 20 varieties of *Lolium* to aluminium toxicity, with a view to using this as measure of adaptation to acid soils, showed that individual plants within most varieties had unusual resistance, also that they varied in resistance. This was shown for shoots and roots by visual scoring and by percentage decrease in yield from the control. Data for six representative varieties are as follows:

The percentage decrease in seedling shoot and root weight of strains of L. perenne *in response to a toxic level of aluminium*

Strain	*Percentage decrease in* *Shoot weight*	*Root weight*
A	64.3	74.4
B	28.1	75.0
C	0.0	53.0
D	76.5	68.1
E	39.4	39.7
F	3.2	42.9

The percentage reduction in yield of shoot and root is not necessarily correlated in any one variety, thus pointing to the fact that at least partial resistance to aluminium toxicity in ryegrass may be a translocation effect.

It has been demonstrated (Vose and Koontz, 1959) that within *T. repens* there is considerable variation in the ability of strains to accumulate calcium in the leaves. Thus when grown on soil with a high calcium content S.100, Dutch and Ladino white clovers were not significantly different in their calcium content, but on two other soils with lower calcium content S.100 had significantly less calcium than the other two varieties:

The calcium content and yield of three strains of T. repens *grown on three soils of different calcium content*

Variety	*Soil A*		*Soil B*		*Soil C*	
	Ca $\mu e/g$	*Yield* (100)	*Ca* $\mu e/g$	*Yield* (*rel. to A*)	*Ca* $\mu e/g$	*Yield* (*rel. to A*)
S.100	1020	100	521	91	755	89
Ladino	976	100	770	77	1050	77
Dutch	995	100	770	67	985	49

We know from practical experience that S.100 does well on hills of relatively low calcium status and we might therefore conclude that S.100 has a low requirement for calcium and that Dutch and Ladino have a high requirement, but the picture is more complicated. A study of the yield shows that the yield of Dutch declines much more on the low calcium soils than does that of S.100 and

Ladino. The indications are, therefore, that there are at least three classes of white clover plants ; those with low uptake and low requirement (S.100), those with high uptake and high requirement (Dutch), and those with high uptake and comparatively low requirement (Ladino).

GRASS BREEDING

A. R. Beddows

The effect of varying the numbers of parent plants on the behaviour of synthetic varieties (E.L.B., E.J.L.)

In a synthetic variety based on unrelated self-sterile plants the decline in vigour after the first generation will be proportional to the amount of inbreeding brought about by the intercrossing of related plants. The frequency of this intercrossing will be largely controlled by the number of unrelated plants on which the variety is based. The yield after three or four generations of multiplication will depend, therefore, not only on the ability of the basic plants to combine well together, but also on the number used.

In 1953 data were available on the forage yield (hay and aftermath cuts) of all possible single crosses deriving from seven early-flowering unrelated plants of perennial ryegrass. The parent plants were ranked according to the average behaviour of their progeny and 15 experimental varieties were constructed, as indicated in the figures on p. 22.

The varieties fall into six groups which depend on the number of basic plants. Within each of the first five groups the varieties differ in the combining ability of the parents. Thus varieties 1, 5, 8, 10 and 12 are founded on the combination of plants of appropriate number giving the highest yielding progeny, and varieties 4, 7, 9, 11 and 13 on the combination giving the lowest yielding progeny. In the groups based on 2 and 3 plants there are additional varieties (Nos. 2, 3 and 6) which are founded on combinations of plants giving progeny with intermediate yields. The seed produced from the single crosses was taken as first generation (Syn. 1) seed, the varieties with more than 2 basic plants being built up from equal proportions of all possible constituent crosses. This method was applied also to one 7-plant variety (No. 14). Normally Syn. 1 seed would result from a polycross and if there were any differences in the seed- or pollen-producing capacities of the parents such equal representation would not be obtained. As a check on this, an additional variety (No. 15) was founded on the seed deriving from the polycross of all seven plants.

The average yields of single crosses (g. green weight/plant) entering into the construction of the different varieties are given in the following figures and are estimates of Syn. 1 yields in 1953.

Structure of the synthetic varieties and their average yields in 1953 and 1959

1953 : 1st generation (Syn. 1) values, g. green weight/plant, 2 cuts (hay and aftermath)
1959 : (Syn. 1) and (Syn. 2–4) values, g. dry weight/plant, single hay cut

		Number of basic plants used in constructing the varieties																
		2				3			4		5		6		7			*L.S.D.* (5%)
	Variety No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	*S.*24	
1953 Green wt. (g)	Syn. 1	1032	782	723	502	941	791	561	879	663	845	706	805	734	774	—	—	
1959 Dry wt. (g)	Syn. 1	157	165	180	151	171	168	149	184	124	174	155	171	155	155	151	139	27.2
	Av. Syn 2–4	147	136*	123*	91*	150*	126*	104*	170	120	156	132*	140*	133*	139	148	141	15.7
	Comparison of Syn. 2–4 rel. to Variety 14 = 100	106	98	89**	66**	108	91	75**	122**	87**	112**	95	101	96	100	107	102	

Least significant difference (L.S.D.) at 5% level for columns = 20.0
*Significant decrease in yield from 1st to subsequent generation ($P < 0.05$)
**Significantly different from control = Variety 14 ($P < 0.05$).

The varieties were multiplied for a further three generations, the seed from each generation being stored in a refrigerator to preserve viability and ensure that ultimately it would be possible to compare simultaneously all varieties for each stage of multiplication.

In 1958 material from all four generations of the 15 varieties was put out in the field as spaced plants and broadcast plots. The two parts of the experiment each included material from four multiplicative generations of S.24 as a control, and were arranged in a randomised block lay-out with five replications. All blocks contained 16 main plots, each occupied by a different variety and split into four for the separation of generations. A number of measurements was made during 1959, including the yield of the material cut for hay on 21–26 May (approximately 4 weeks after the mean date of ear emergence). In this preliminary review of the results the discussion will be restricted to data deriving from the dry weight of spaced plants for this single hay cut.

Each sub-plot contained 20 spaced plants but only the first five were dried and consequently the analyses of variance are based on the means of these five plants. The complete analysis (Generations 1–4) is as follows:

Analysis of variance of yields of dry matter
(hay cut 21—26.5.59)

	Generations 1–4		*Generations 2, 3, 4*	
Source of variation	*N*	*M.S.*	*N*	*M.S.*
Replicates	4	890	4	672
Varieties	15	5510*	15	5569*
Error A	60	711	60	623
Generations	3	12407*	2	321
Generations × varieties	45	738*	30	473
Generations × replicates	12	404	8	400
Error B	180	381	120	387

*P <0.001

The differences between varieties and generations are highly significant. Their interaction is also significant at the 0.1% level so that the change from generation to generation is not a consistent feature of all the varieties. If the first generation is excluded from the analysis (Generations 2, 3, 4), only differences between varieties remain significant. Thus all changes in varieties associated with

seed multiplication must have taken place during the first generation of increase, i.e., between Syn. 1 and Syn. 2. In other words all varieties have stabilised by Syn. 2 and therefore the last three generations can be pooled to provide a single estimate of the final yield.

The 1959 varietal mean yields for Syn. 1 separately and an average value for Syn. 2–4 are included in the table on p. 22. It is of interest first to compare the Syn. 1 values for 1953 and 1959 ; Var. 15 is necessarily excluded from this comparison. The correlation coefficient (0.49) is positive but barely achieves significance at the 5% level. A number of factors are operative in reducing any correlation between these sets of figures, including differences in the number of cuts and methods of weighing as well as year-to-year interactions. Nevertheless the correlation within groups is good except for Varieties 1 and 3 in the first group, and if these are excluded the overall correlation considerably improves ($r = 0.70$ and $P = 0.01$). On the other hand, the correlation between the 1953 Syn. 1 values and the 1959 Syn. 2–4 final yield estimates is surprisingly high ($r = 0.86$ and $P < 0.001$). Indeed this is higher than the corresponding correlation using 1959 Syn. 1 values ($r = 0.57$ and $P = 0.05$-0.01) although the latter is considerably improved if Varieties 1 and 3 are again omitted ($r = 0.70$ and $P = 0.01$) and this suggests that the 1959 Syn. 1 values for these two varieties should be treated with some caution. Such a comparatively lower correlation for comparisons within the same experiment and year admits of no simple explanation, unless a differential deterioration of Syn. 1 seed during storage is postulated. This aspect, however, need not concern us too much since whether Varieties 1 and 3 are excluded or not the difference between the two correlations does not achieve significance. In either case the comparisons clearly demonstrate that the final yield of the varieties is at least partially a function of the combining ability of the parents, as measured by the yield of first generation single crosses.

Further consideration of the 1959 data is more informative. If we reject Variety 1 on the grounds that the Syn. 1 value might be anomalous, then all varieties based on 2 plants and 3 plants show a significant decrease in yield from the Syn. 1 to subsequent generations (see table). For the 4-plant varieties this decrease is only slight and not significant. One of the varieties based on 5 plants and the two based on 6 plants, however, show a significant decrease so that evidently the results for the varieties based on 4-plants are not merely a function of the basic numbers but must also reflect the genetic constitution of the parents. Later it is hoped to relate these

findings more explicitly to the genetic constitution of the parents as assessed by the analysis of a diallel cross grown in two different seasons. For the moment it suffices to establish the importance of the genetic constitution of the parents in relation to the basic numbers required to maintain vigour during multiplicative generations.

In the comparison of Syn. 2–4 values (see table) the final yield rating of the varieties is given in relation to Variety 14 based on 7 plants = 100. It will be noted that at no stage does Variety 15, founded on polycross seed, differ from Variety 14, constructed initially from single cross seed, so that there is no evidence of gross differences in pollen- or seed-producing capacities among the parents. One of the varieties based on 2-plants and one based on 3-plants rate slightly, but not significantly, higher than control, while altogether four varieties in these two groups are not significantly different from control. Thus by selecting among the initial seven parents it was possible to reduce the number of basic plants to two without any sacrifice in final yield, thereby greatly facilitating the prospects of more rigorous selection of characters other than those directly associated with yield. Variety 8, based on four plants selected for high average combining ability, significantly outyields control and is considerably better than the next highest yielding variety which is based on five plants. In this material, therefore, which Lewis (W.P.B.S. Rep. 1956–58, p. 7) has shown to exhibit only general combining ability, the most efficient number of plants for a synthetic variety is four.

It may be noted that at the date of cutting in this particular year S.24, which was included as a standard, is significantly outyielded by two experimental varieties. All the seven plants under consideration were earlier flowering than the mean date for S.24 so that the hay cut, based on the mean flowering date for the whole experiment, was taken before S.24 had achieved its maximum growth.

The results, in so far as the hay cut is concerned, conclusively demonstrate that the most efficient number of plants for a synthetic variety is considerably less than was originally thought desirable. This provides possibilities not only of exercising a more rigorous selection, but also of reducing the time and labour involved in the maintenance of basic plants. The necessity of an adequate method of progeny testing is, however, emphasised and it may well be that in the final stages of selection the increased information deriving from a diallel cross will more than offset the lower labour requirements of other systems of progeny testing.

Leaf development in Gramineae (M.B.)

The size of the grass leaf, especially the blade, is important in relation to herbage production, and in *Glyceria* has been shown to be useful for the identification of varieties (*Watsonia*, 4, 77–88, 1957). A knowledge of the anatomical, developmental, and genetical basis of variation in leaf size is therefore of interest.

Blade size was studied in successive leaves on the flowering shoot in species of *Glyceria*, *Lolium* and *Triticum* (Borrill 1959). The blades of successive leaves were progressively larger, eventually reaching a maximum, after which those of the last few leaves produced before heading were shorter. When the largest leaf blade was elongating, dissection of the shoot apices showed that inflorescence initiation was taking place. In *Triticum* epidermal cell measurements indicated that differences in blade length are due to differences in the amount of cell extension.

In *Lolium temulentum* leaf and cell sizes were recorded for leaves on the flowering shoot. The duration of low temperature pre-treatment applied affected the relation between blade and sheath length and width in successive leaves so that the ultimate leaf (the flag leaf) had a larger area than the preceding ones. In all cases the length of the sheath increased progressively, a spectacular increase occurring in the last one or two leaves. Variation in the relative proportions of blade and sheath in different conditions maintains the total area of the flag leaf at an approximately constant value. This may be related to the importance of the flag leaf in the nutrition of the ear in this cereal-like grass.

Underlying these morphological changes is a cell pattern. The length of the blade is related to the length of the epidermal cells, as in *Triticum*, whereas blade width depends directly on the number of rows of cells in the width of the leaf.

In the earlier leaves, the length of the sheath tends to be based on the length of the cells. In later sheaths formed after the initiation of the inflorescence, this trend is reversed, the length of successive sheaths increases rapidly, and is associated with a decrease in cell length, which implies that the cell number is increasing.

It appears that a correlated change occurs in leaf morphology associated with the onset of the reproductive phase at the shoot apex. In the blade this is brought about anatomically in two ways, in length by means of degree of cell extension, and in width by variation in cell number. This suggests that blade length and width may be independently inherited. It is clear that for leaf size to be of

value in varietal identification, sampling should be selective, and the comparisons made under similar environmental conditions.

The control of algae on earthenware pots (A.R.B., D.E.S.)

Replicated tests were undertaken to ascertain if an effective system could be evolved for the removal of algae on earthenware pots other than by scrubbing with hot water. The evidence suggests that dipping pots in 2% copper sulphate solution for not less than five minutes provides a disinfecting deposit which will give an effective and easy method of pot cleaning and will not interfere with normal growth. The full results will be published elsewhere in due course.

The work on cocksfoot streak (A.R.B.) and on "stunting" in *Lolium perenne* (A.R.B., D.E.S.) is included under Plant Pathology.

LEGUME BREEDING

W. Ellis Davies

The breeding potential of white clover populations from different parts of the world (W.E.D., N.R.Y.)

Indigenous white clover from the best pastures in England and Wales has a restricted range of variation and can be classified in the small-leaved group. Kent wild white is an example of this and while this variety is very persistent under hard grazing it does not have the yield potential of the medium-leaved group, e.g., S.100 and New Zealand white clovers, which have been termed cultivated types.

There are no indigenous large-leaved types like Ladino in the British Isles, therefore breeding material must be obtained from overseas. White clover has a distribution extending from the Mediterranean to the Arctic and in other temperate zones throughout the world. In order to have some information on a possible source of supply about 60 selected populations, some of which were used by Daday (*Heredity*, 8, 61–78) in the survey of cyanogenetic glucosides, were grown as spaced plants. Data were collected on spread, plant height, leaf size, flowering date and weight.

Similar clines to those noted for lotaustralin and linamarase alleles were observed for leaf size and plant height. Plants from the Mediterranean populations came into the large-leaved group, while those from high latitudes or altitudes were in the small-leaved group. Many were in the medium-leaved group, e.g., populations from Normandy and New Zealand. It appears that the cultivated types now used in Britain have been derived from the multiplication of clover from this intermediate type. Differences were also observed in time of flowering with a general trend towards lateness in the northern populations. The range of flowering was, however, less than in red clover.

A comparison of wild and cultivated red and white clovers shows that red clover types are quite distinctive, the wild being very stemmy, whereas the cultivated forms are leafy. There is no comparable difference in white clover, the wild type although smaller in size is as leafy as the cultivated. It may therefore be feasible to locate populations which by natural selection have reached a sufficcient degree of stability to be used for the production of new varieties. There appears to be ample scope in white clover plants for explorations of this kind.

The effect of F_1 selection on the subsequent yield of white clover families (W.E.D.)

In an outbreeding species each plant is equivalent to an F_1, while crosses of two unrelated plants result in the production of a new F_1. Selection in the absence of inbreeding is, therefore, based on F_1 and it is desirable to know the effect of such selection on the subsequent performance of that line.

Plants from six F_1 families were classified into good and poor on the basis of their vigour. This initial classification was checked by taking cuttings of the selected plants and replanting in a replicated experiment. The correlations between the initial selection and the results from the replicated cuttings were often poor. Crosses were then made within each family, and the figures show the relative mean yield of F_2 families (g = good, p = poor) :

	g × *g*	*g* × *p*	*p* × *p*	
Relative yield of F_1 parents	100	—	27	
Relative yield of F_2 families	100	108	97	N.S.

It is clear that selection of the F_1 family into good and poor made little difference to the yield of the F_2 families. Selection into good and poor was again carried out in the F_2 families, the good plants being the highest yielders, the poor producing less than the mean for the family. Crosses were made between good and poor plants within a family and also with four unrelated tester plants from another F_1 family. Yields of F_3 families are given relative to those of the outcrossed families = 100.

	F_2 families from			
F_3 families from	*g* × *g*	*g* × *p*	*p* × *p*	*Mean*
g × *g* F_2 plants	108	82	105	103.8
g × *p* ,, ,,	93	91	70	87.4
p × *p* ,, ,,	78	91	70	78.5
Mean	93.3	89.0	87.8	90.3

Estimated L.S.D. 5% Means = 12.4
Rows, columns = 21.6

The F_3 families showed a yield depression of 10% compared with outcrosses. Selection in the F_1 families (column means) again

showed no significant difference, but selection into good and poor in F_2 was more successful, there being a large difference between g × g and p × p crosses (row means). There were even larger differences evident in the body of the table, showing that selection in F_1 and F_2 for good plants had given an increase of 38% over similar selection for poor plants.

Outcrossing the good and poor F_2 plants to the four unrelated testers restored the F_1 situation, and the mean yields of good and poor outcrosses were 99.2 and 101.7 respectively. The means of the crosses involving the four outcross-testers were 103, 99, 98 and 102.

The assessment of breeder's material (W.E.D., B.T.)

Lucerne. This crop is often grown without a companion grass and harvested by cutting three times a year. A simple assessment technique can therefore be used leaving one major variable, i.e., the spacing of the individual plants. There are large numbers of selections to be tested and the amount of seed is small, therefore, to make the best use of the available material space-planting must be adopted. A previous experiment has shown that the normal spacing of 24 ins. × 18 ins. gave an unsatisfactory correlation when compared with results from broadcast sowings. A further experiment was therefore set up where spacings of 3″ × 3″, 6″ × 6″, 12″ × 12″ and 24″ × 18″ were compared with a control broadcast plot. The closest spacing gave the best correlation with the sown plot, and as spacing became wider the relationships became less satisfactory. Yields of dry matter were very similar in the broadcast plot and in 3″ × 3″ spacing ; they were slightly higher at 6″ × 6″ and smaller at 12″ × 12″ and 24″ × 18″, the latter being about 40% of control.

The capacity for tillering appeared to be the major factor involved. Differences between varieties at the close spacing were small because of the effect of inter-plant competition, but at the wider spacing, and in the absence of competition, maximum tillering could be expressed.

From this work the optimum spacing appears to be between 16 and 4 plants per sq. ft. Further work is in progress to elucidate this point. It is interesting to note that in practice when lucerne is sown broadcast at 20 lb./acre in June, 26–40 plants per sq. ft. establish by August. By the following April this is reduced to between 10 and 20, a year later to 8–13, and subsequently to 7–11. This would suggest that the equilibrium is reached around a mean of 10 plants per square foot.

Seed setting in tetraploid red clover (A.M.E.)

The summer of 1959 was ideal for seed setting in clover but in spite of this, the seed-set of polyploid clovers was rather poor. Low fertility is an important problem to overcome in breeding autopolyploids, and investigations have been made into three aspects of this problem.

1. Corolla tube length was measured in diploid and tetraploid families of red clover in the field. The mean length in the diploid was 9.2 mm. with a range of 7.8–10.6 mm. In the tetraploid, mean length was significantly greater, being 10.2 mm. with a range of 8.4–12.8 mm. This suggests that long corolla tube may be one factor responsible for the low degree of pollination in the field.

2. Seed setting was compared after hand-pollination in the glasshouse and open-pollination in the field in Aberystwyth S.151 and S.123 diploid red clovers and five tetraploid families.

	Mean seed number per head	
Family	*Hand-pollination*	*Open-pollination*
S.151 (2x)	48.5	44.0
S.123 (2x)	67.3	52.6
Tetra 1	40.6	26.2
2	34.2	22.8
3	27.4	17.1
4	46.8	21.9
5	41.5	12.9

The seed set after hand-pollination was appreciably higher than after open-pollination. This is due partly to climatic conditions in the field, partly to the ineffectiveness of pollinating insects, and partly to the presence of abortive triploid embryos produced as a result of inter-pollination of diploids and tetraploids.

3. Irregularities between fertilisation and full embryo development were considered. It was observed that often embryo development was interrupted, and some tetraploid embryos aborted about 15–18 days after pollination. By artificial culture, these embryos could often be salvaged and grown successfully to mature seedlings.

	Head 1	*Head 2*
	Mean seed No.	*Mean No. of viable embryos*
Cross	*per 100 florets*	*per 100 florets*
A × B	60.0	73.5
B × C	55.4	77.2
A × C	46.9	71.9

Head 1 was allowed to set seed normally while embryos from florets of Head 2 were excised 15 days after pollination. It was possible to culture most of the embryos, yet abortion of comparable embryos took place in the head allowed to set seed normally. This suggests that the embryo itself is normal, and that abortion occurs because the embryo lacks nutriment, probably due to an ineffective endosperm. Detailed embryological studies will be made to clarify this point.

The work on white clover viruses is included under Plant Pathology.

CEREALS, BEANS AND *BRASSICAE* BREEDING

D. J. Griffiths

THE CEREAL CROPS

The basic aim of every cereal breeding programme is to improve still further the yielding potential and quality of these crops through the development of new varieties which can be more fully exploited by modern husbandry practices and increased farm mechanization. Of necessity such an objective involves a continuous long-term programme of hybridization, selection and extensive field testing. At this Station increases in yielding ability are being sought in the spring and winter oat crops, and in spring barley and spring wheat through direct improvement of what may be described as yield characters, as well as by reducing the effect of factors which limit yield in the field. In practice the two approaches cannot be separated but they receive a different emphasis in the various crops, depending on needs in terms of varietal requirements.

OAT BREEDING INVESTIGATIONS

Production of new disease-resistant varieties (D.J.G., D.G.R., J.D.H., I.T.J., W.T.H.P.)

The year under review marks an important stage in the oat improvement work, namely, that of the official recommendation by the National Institute of Agricultural Botany of two new Station-bred varieties, Pennant S.227, a general-purpose, high-yielding, stem eelworm-resistant winter variety, and Manod S.235, a general-purpose spring variety possessing resistance to mildew, crown rust and stem eelworm. Details of the breeding history and varietal characteristics appear on pp. 69 and 70.

The new winter hardy variety Pennant is higher yielding than S.147, shorter and stiffer in the straw, and because of its high degree of resistance to stem eelworm attack it is specially recommended in place of susceptible winter varieties wherever the nematode is suspected. Its resistance to eelworm attack is well illustrated in the frontispiece, which depicts Pennant growing alongside a susceptible variety in a heavily infested field, and where it subsequently yielded approximately 30 cwt. of grain, compared with a complete crop failure of the susceptible variety. Under conditions such as these the

growing of a resistant variety not only ensures a full crop but also restricts any increase in the nematode population by preventing further multiplication within the plant tissues, as well as preventing the establishment of various arable weeds which also act as hosts to the eelworm.

The spring oat variety Manod exhibits a high degree of resistance to stem eelworm (*Ditylenchus dipsaci*), mildew (*Erysiphe graminis avenae*) and crown rust (*Puccinia coronata*), and thus represents the first variety possessing resistance to all three diseases to be made available to the British farmer.

Evidence of its capacity to withstand stem eelworm attacks under field conditions was obtained in 1959 from Davies† in North Wales, and from White† in the North of England. The comparative figures (unpublished) obtained by White for eelworm infestation and resultant yields in respect of Manod and Sun II for three replicates of a trial sited on infested land were as follows :

Replicate	*Percentage plants affected by eelworm*		*Relative grain yields per plot (lb.)*	
	Sun II	*Manod*	*Sun II*	*Manod*
a	7.7	0.0	56.5	65.0
b	23.6	1.4	49.5	66.5
c	26.3	0.0	47.0	60.0

The relative general yielding capacity of Manod in relation to other varieties in stem eelworm-free soils in seasons of light and heavy mildew attacks is illustrated by results previously published (Griffiths 1959), which are reproduced below :

Mean yields of grain from mildew resistant and susceptible oat selections, 1953 and 1954

Variety or selection	*Reaction to mildew*	*Grain yield*	
		1953	*1954*
		Slight mildew attack	*Heavy mildew attack*
		cwt./acre	
Sun II	Susceptible	26.9	21.8
S.84	,,	27.9	18.7
4757/6/2/19	Resistant	29.2	30.5
4757/18/2/19 = Manod	,,	30.1	29.2
Sig. diff. (P = 0.05)		3.93 (n.s.)	3.43

†Regional Advisory Entomologists, N.A.A.S. (Wales) (Sub-centre Bangor) and Northern Region.

The figures not only show the superiority of the resistant variety over susceptible forms under heavy disease conditions but also provide an indirect measure of the losses which can be incurred from a serious attack of mildew.

Crown rust, and especially mildew, are two of the most common and widespread fungal diseases of oats in the South-West and Western regions of England and Wales, and when conditions are favourable for their early development and spread the losses caused can assume quite serious proportions, as was experienced in 1954.

When crops are heavily attacked by mildew loss occurs in both quality and quantity of grain, and in bad mildew years the leaves may become so covered with the fungus that the palatability of the straw is impaired. This latter aspect is an important consideration on upland farms where oat straw is a much valued winter fodder. This new variety should thus prove of special value in those areas which regularly experience heavy attacks of mildew, for even under relatively disease-free conditions the variety compares favourably with Sun II in general yielding and standing ability.

Another important feature of mildew resistance which has been observed in the course of field testing is the correlation which exists between a heavy infection and lodging, with consequent effect on grain yield, quality and ease of harvesting. In damp seasons saprophytic fungi readily invade the slowly maturing tissues of susceptible varieties after severe attacks of mildew, thus rendering the straw extremely brittle and liable to break before the crop attains full maturity. As a result the grain does not fill properly, harvesting is made difficult and the straw is of little value for feeding. Mildew resistant types, on the other hand, are far less affected by these secondary infections, and in consequence the straw retains its resilience and capacity to support the crop until it is fully ripe.

Although spring varieties are the more seriously affected by mildew, nevertheless it is considered highly desirable to introduce resistance into winter varieties also, since the autumn sown crop serves as the overwintering host for the fungus and thus provides a reservoir of inoculum for an early infection of the crop sown in the spring. The importance of the winter crop in relation to the incidence of mildew on the spring crop and its detrimental effects is well appreciated in certain countries on the Continent where the growing of winter barley is discouraged in order to reduce the early spread of mildew on spring barley.

Several promising winter-hardy, mildew-resistant oat selections were under advanced test at the Station in 1959 and, in addition,

favourable reports were again received from the N.I.A.B. on the general performance of Station selection No. 5370 Cn 2/2/41, as well as on the two new stiff-strawed lines E.2296 and E.2297, which possess resistance to both stem eelworm and mildew.

In relation to the disease breeding programme it is also gratifying to report that root eelworm investigations conducted in collaboration with the Advisory Entomologist N.A.A.S. (Wales), Bangor Subcentre confirmed previous observations indicating a potential source of resistance for breeding purposes in certain *A. sterilis* forms, and root cyst counts made on derived hybrid material indicated its successful transfer through backcrossing into *A. sativa* types.

Irradiation studies with winter oats (D.J.G., T.D.J.)

The production of mutations in cereals by means of ionising radiations has been extensively studied in recent years especially in Sweden and the United States. As a technique in plant breeding the method has certain theoretical advantages in that it offers the possibility of inducing rapidly fixable improvements in a single character of a variety by altering only small hereditary units, whilst leaving unchanged the general genetic make-up of the plant. Relatively little research, however, has been carried out on the efficiency of the method in routine breeding for achieving improvements in quantitatively inherited field characters, when compared with close intervarietal hybridisation in a hexaploid crop such as oats. In 1954, therefore, an experiment was commenced to assess the value and limitations of such a technique on two Station-bred varieties of oats.

The varieties selected for study were S.147 and S.172. Both are widely grown winter varieties but each has a drawback, in S.147 it is an excessive straw length for modern conditions, and in S.172 it is grain of below-average size. Accordingly attempts were made in the present experiment to improve characters of this nature as well as screening the material for other agronomically desirable variants.

Initially, 600 X_1 plants of S.147, and 400 of S.172, were grown after the irradiation of dry seeds with X-rays and Gamma rays from a Co^{60} source. From approximately 6,000 progeny rows in the X_3 generation the numbers were finally reduced to 23 lines of S.147, and 11 lines of S.172 in the X_5 generation, the earliest stage at which sufficient seed was available for precise replicated trials. The following table summarises the performance of some of the X_5 generation lines compared with the unirradiated mother varieties :

Performance of some X_5 generation lines of S.147 and S.172 in replicated trials compared with unirradiated controls

Line	*Heading height (ins.)*	*Heading date (days after control)*	*Yield (% of control)*	*1,000 grain weight (g.)*
S.172				
Control	24.0	0	100	27.9
1	17.4*	+4½*	60*	28.5
2	22.1*	0	94	28.2
3	22.1*	− ¼	95	27.5
5	22.2	+ ¼	102	28.3
6	23.1	0	86*	28.4
7	26.3*	−2*	96	31.7
8	23.8	−1¼	89	29.1
12	23.6	−2¼*	87*	33.4*
S.147				
Control	27.9	0	100	—
2	25.9	+2½	84*	—
3	24.8*	−1¼	93	—
4	24.1*	+1¾	80*	—
10	28.6	+ ¾	99	—
12	26.3	−4*	92	—
13	23.6*	+1¾	87	—
17	25.8	−1¼	104	—
19	26.5	− ½	108	—
24	25.2	+1¼	76*	—
25	27.1	+ ½	108	—

*Significant difference from control (P = 0.05)

These results indicate clearly that agronomically interesting variants have been isolated although none was found with yield significantly greater than the original varieties. This experiment shows that potentially useful variants can be produced, but emphasises the practical difficulties consequent upon the random nature and low frequency of the mutation process, necessitating the very large numbers of progenies, and also the difficulty of selecting for quantitative characters on a single plant or single row basis. Thus if viewed strictly in terms of the potentially useful mutants derived in relation to the land and labour devoted to the experiment it seems

unlikely that, in the oat crop where a wide range of variability already exists, mutation breeding can replace the normal hybridisation and selection techniques.

BARLEY

Breeding investigations (J.D.H.)

The recently initiated spring barley breeding programme was further expanded in 1959 to include the most promising disease resistant genotypes, special attention being given to mildew resistance. The most striking developments in the barley work during the year under review were the discovery of the clear-cut differential response of various commercial varieties to DDT spray and that the reaction is controlled by a single major gene with susceptibility to damage being dominant to resistance.

A large number of varieties were screened for reaction and from the results it is clear that the presence of the resistant gene in present-day varieties is entirely fortuitous, depending on whether one or both of their parents carried the factor in the first instance. There is also no suggestion to indicate that this factor has had any selective influence in previous plant breeding programmes or that reaction is associated with any gross morphological feature of the barley plant.

In view of the clear-cut differential responses manifested by some of the leading varieties, such as the complete resistance of Proctor on the one hand, and the susceptibility of Rika on the other, spraying with DDT can provide an effective means whereby varietal stocks may be quickly assessed in the seedling stage for any admixture of varieties exhibiting a different reaction. Furthermore, the technique may also be used on a field scale for the removal of susceptible 'rogue' plants from stock plots of resistant varieties.

Information on varietal reactions to DDT spray, together with the results of other investigations conducted to date and their implications in relation to breeding, are given in greater detail elsewhere (Hayes, 1959).

Cereals for forage production (J.D.H.)

In spite of the achievements of plant breeders in developing strains of grasses that will provide forage practically all the year round, February and March still prove the most difficult months, and quite frequently farmers are forced to graze forward fields of

autumn sown cereals to offset the shortage of keep during this period. Recent work at the Station has been designed to assess the potentialities of winter cereals to fill this need for early spring grazing.

Over forty winter-hardy forms of wheat, barley, oats and rye have been assessed for their winter forage production and as indicated in the following table the winter ryes as a group clearly appear to be the most promising:

Forage production by the four species of cereals in early spring 1959

Species (winter varieties)	*Dry matter production in relation to winter oats*	*Percentage crude protein*
Rye	164	15.5
Wheat	107	19.9
Oats	100	16.9
Barley	96	18.4

Within the rye species there are many varieties now available commercially in Britain which differ markedly in their performance as forage producers. These can be broadly classified into groups according to their origin and the results presented below serve to indicate the superiority of forms derived from Central Europe:

A comparison of the forage production of various rye stocks in relation to winter oats

	Defoliation dates		
Varietal group and origin	27/3/58	14/4/59(a)	14/4/59(b)
Central European ryes	248 (4)	200 (1)	266 (5)
English ryes	199 (2)	129 (1)	188 (1)
Tetraploid ryes	200 (2)	—	—
North European ryes	132 (2)	—	—
Winter oats	100 (13)	100 (6)	100 (1)

(a) and (b) = two distinct trials
Figures in brackets = number of varieties tested.

The Central European group appear able to make growth at lower temperatures than other cereals and to maintain steady growth through the early spring, but they are low tillering and require a high seed rate to produce their maximum yields. The present rye breeding programme is designed to develop higher tillering varieties with the same capacity for growth under low temperatures as the Central European types, as well as being able to respond to

early dressings of nitrogen. The first cycle of selection towards the development of such varieties was undertaken in the past season.

BRASSICAE CROPS

The kales and rapes occupy an increasingly important role in British agriculture, and over the past two decades the acreage devoted to these two crops in Wales alone has increased nearly fourfold to the present-day total of nearly 80,000 acres. As in other regions, some of this impressive increase has been at the expense of root crops such as mangolds, which are becoming less popular under modern conditions of farming because of the high labour requirements for thinning, lifting and clamping. The kales and rapes, on the other hand, are capable of high yields of succulent green feed which can be consumed *in situ*, and one of the major long-term programmes of work being undertaken at the Station with these two crops is to extend still further their usefulness for winter grazing under lowland and upland conditions, by developing new strains with better winter hardiness and improved leaf-retaining capacity.

Kale investigations (T.D.J.)

During the past season five strains of thousand-headed kale were grown in a replicated trial at a lowland centre, and in an exposed situation at an altitude of approximately 700′, for evidence of possible strain × locality, or strain × harvest date, interactions to provide data upon which to base future breeding work in relation to edaphic and climatic conditions. Early and late harvest samples were taken from each trial and the figures examined for yield of leaf and percentage leafiness. The results given below indicate that although yield and leafiness were generally lower at the higher altitude, and that there was a greater loss of leaf at this centre between the dates of harvesting, there was no apparent differential varietal response to the two sets of conditions.

Leaf yield (tons/acre) and percentage leafiness of 5 commercial strains of thousand-headed kale grown at 2 localities

	Leaf yield				*Percentage leafiness*			
	Lowland		700′ *altitude*		*Lowland*		700′ *altitude*	
	Harvested							
Strain	9.12.58	27.1.59	8.12.58	27.1.59	9.12.58	27.1.59	8.12.58	27.1.59
A	3.94	3.32	4.25	2.95	72	68	65	58
B	4.40	3.84	4.06	2.79	69	65	64	55
C	4.36	3.81	4.16	3.00	74	69	70	63
D	4.34	3.58	4.15	2.94	68	58	63	52
E	5.48	4.73	4.90	3.25	72	69	69	58

Rape investigation (T.D.J.)

One of the most troublesome diseases of *Brassicae* crops, and particularly rape, is clubroot or "finger-and-toe" caused by *Plasmodiophora brassicae*. The pathogen is soil-borne and difficult to control effectively by chemical or cultural means. Foreign strains of rape exhibiting a measure of resistance to the disease are known to exist and have been employed in a programme of hybridisation with the well-adapted British strains. Tests on clean and infected land have clearly shown the value of introducing resistance into the crops as indicated by the results given below :

Dry matter yields (cwt./acre) of two native strains of rape and their hybrids with clubroot resistant types

Strain	*Dry matter yield on*	
	Heavily infected land	*Non-infected land*
Native Strain A	6.4	29.4
„ „ B	4.6	31.9
A × resistant type	17.8	34.2
B × resistant type	17.8	33.1

The above figures from replicated trials indicate that on non-infected land the yield of dry matter from the hybrid populations, derived through crossing native adapted strains with the clubroot resistant type, was nearly identical, whereas under infected conditions the two hybrid lines gave greatly superior yields. The lower yield obtained in the hybrids on the heavily infected land, compared with their performance on the clean area, however, was due almost entirely to the lower inherent fertility of the former centre.

Preliminary experiments on a male gametocide (T.D.J.)

Preliminary trials with a male gametocide which has been used with success on *Gossypium* have been carried out on kohlrabi (*B. oleracea* var. *gongylodes*) and giant rape (*B. napus*).

After introducing a range of quantities of the chemical into kohlrabi plants in the glasshouse it was found that various effects were produced including (at a dosage of 0.04 g./plant of approximately 200 g. green weight) complete functional male-sterility with little effect on ability to set seed following cross-pollination. At this particular concentration most of the pollen grains appeared non-functional and anthers were small and failed to dehisce over a

period of about 4 weeks. Higher concentrations produced marked phytotoxic effects causing severe distortion or death of many unopened buds.

In rape the preliminary experiments indicated that the phytotoxic effect occurs before male sterility is achieved.

Further research on this substance is necessary to ascertain whether it can be used on a field scale to induce male sterility in the *Brassicae* crops.

GRASSLAND AGRONOMY

Ll. Iorwerth Jones

The behaviour and production of potential herbage varieties continue to receive considerable attention. Their performance under varying conditions which also involved different managements and fertiliser applications was compared with varieties normally used in agriculture in order to indicate the conditions most favourable for their full exploitation before their release as new varieties.

In agricultural practice plants are seldom allowed to develop without defoliation by man and/or the grazing animal. The date and intensity of defoliation, coupled with density of plants and fertiliser application, have a marked influence on recovery growth. When defoliation removes or damages the growing apex, further growth can only occur by the development of new buds at the base of the tiller, and this growth is considerably slower than in a recovering tiller where the growing apex has not been damaged. Some of the more interesting features of plant and shoot growth are discussed in the two articles, 'Growth stage and related factors in grassland management' by Mr. Ieuan Davies (p. 104) and 'Conditions influencing primary growth and regrowth of perennial ryegrass' by Miss Alison G. Davies (p. 110).

Herbage Assessment Techniques (D.G.M.)

Previous investigations at the Station have shown the importance of sward-conditioning as a factor in the behaviour of herbage varieties, and that herbage plants are influenced to a different degree by the conditions prevailing. Studies were initiated in 1955 to obtain further information on some of these aspects, and to develop simpler and more reliable techniques for herbage variety assessment, particularly methods suitable for evaluating small quantities of plant material such as breeder's selections.

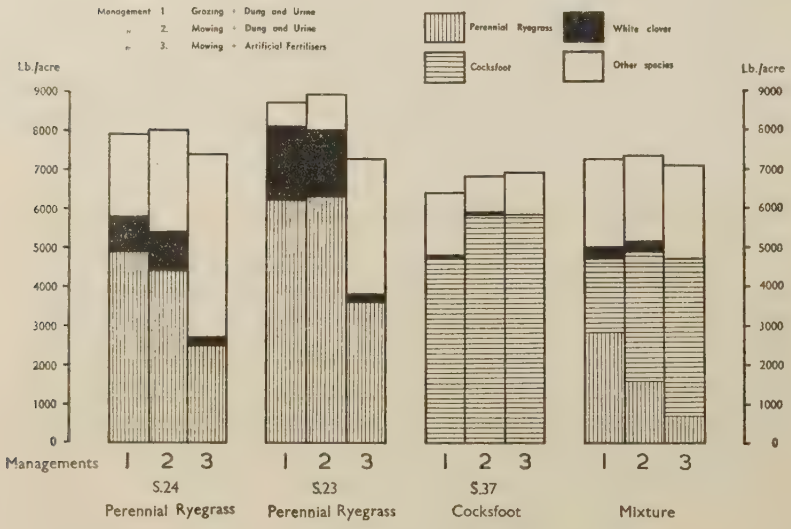
One of the investigations in this series covered a period of four seasons, and was designed to compare the behaviour and production of S.22 Italian ryegrass, S.23 and S.24 perennial ryegrass, S.26 cocksfoot, S.48 timothy each with S.100 white clover, and a mixture of these grasses and white clover. All swards were subjected to six different treatments, involving grazing or mowing, both with and without animal droppings or compensatory quantities of artificial fertilisers.

Portable folds, 10′ × 18′, constructed of aluminium alloy angle covered with chain link fencing were used for controlling the grazing. Normally two sheep, mature Clun wethers, consumed the herbage in a fold in 24 hours. Standard harness was used for the complete collection of dung and urine (Plate 1). Samples for the comparative determination of herbage productivity and botanical composition were taken immediately prior to each defoliation.

The treatments affected the yield and botanical composition of each sward, and the different species and varieties responded in varying degrees and in different directions.

The data for three of the treatments (managements) are given below.

YIELD OF HERBAGE (LB./ACRE)—AVERAGE OF THIRD AND FOURTH HARVEST YEARS



Treatment 1 — grazing with return of dung and urine.

,, 2 — mowing with return of equivalent amounts of dung and urine.

,, 3 — mowing with return of artificial fertilisers containing equivalent amounts of P_2O_5, K_2O and nitrogen.

Plate I

Part of portable fold showing sheep harnessed for collection of dung and urine.

S 22 Italian ryegrass, in the spring of fourth harvest year, showing the effect of dung and urine (*left*) compared with equivalent quantity of inorganic fertilisers (*right*).

Plate 2

Lambs

Yearling ewes

Flock

Sheep reared and maintained on equivalent areas of hill pasture.
Left — from native hill pasture. *Right* — from a 12 year old reseeded hill pasture.

In comparing the influence of grazing and mowing (Treatments 1 and 2) it is observed that the total yield of herbage is almost identical under both treatments. The yield of the cocksfoot component, however, was considerably reduced, particularly in the more complex mixture, whereas ryegrass generally benefited from grazing.

A comparison of the influence of artificial fertilisers as opposed to dung and urine shows that the yield of cocksfoot is almost identical under the two treatments. For the ryegrass swards, on the other hand, the artificial fertiliser gave significantly lower yields of this grass and this was especially marked in Italian ryegrass (Plate 1). In the mixed grass sward the substitution of artificial fertilisers for the dung and urine resulted in a marked decrease in the yield of the ryegrass component and an increase in the cocksfoot.

The total herbage yields, which take into account the contribution of the unsown species as well as that of the white clover, show no differences between fertiliser treatments on the cocksfoot swards. There was, however, a reduction in the ryegrass swards dressed with artificial fertilisers. In general the degree of reduction in total productivity with application of artificial fertiliser can be correlated with the ryegrass and white clover content of the sward.

The data from these investigations are now being fully analysed, but they already serve to indicate the misleading conclusions that may be drawn from assessment of varieties without reference to their performance in a sward under reasonably practical conditions.

Improvement of Hill Pastures (LL.I.J.)

The production from native hill swards is generally low when measured in terms of the number and condition of the stock they are able to maintain. This is due partly to the poor grass species present, coupled with the absence of an effective legume, and partly to the low fertility of the soil. At their best the native swards consist mainly of a mixture of bent and the fine-leaved fescues but the greater proportion of the hills carry swards based on *Molinia*, *Nardus*, heather or *Scirpus* with only a trace of bent. The latter swards are seldom nutritious enough to maintain the ewes in a condition suitable for regular breeding, and on hills where the swards are based mainly on these species the lambing percentage ranges from 60–80% and the lambs produced are generally small and in very poor condition.

Surveys of the grazing habits of sheep on hills in the Aberystwyth area have shown that the intensity of grazing varies con-

siderably from one ecological association to another. This is illustrated by a typical analysis based on observations made on three hill farms over a period of 15 months:

Sward	*Grazing intensity*
Agrostis (bent)	100†
Fescue	62
Nardus or *Molinia*	16
Tall heather	11

† A grazing intensity of 100 for the bent swards corresponds roughly to 1½ sheep/acre/annum.

The above figures were obtained with normal stocking of sheep on the hills and under these conditions the botanical composition of the different areas remains relatively stable.

A change in the rate of stocking, however, produces a significant alteration in the botanical composition of the swards. With a very low intensity of grazing the vegetation deteriorates towards *Nardus* and *Molinia* on the damper areas, and towards heather on the drier areas. Increasing the intensity of grazing, on the other hand, leads to an improvement, e.g., a *Molinia*-dominant sward, one of the most sensitive to grazing, was changed into a bent/fescue-dominant sward within a period of two seasons when subjected to hard close grazing.

Applications of lime and phosphate also bring about a marked change in botanical composition, for two main reasons. The first is that the fertilisers improved the palatability of the native herbage and thereby increased the intensity of grazing, and the second is the direct action of the fertiliser in producing a differential growth of the components. These conclusions may be illustrated from observations made on an unfenced *Molinia* area which was limed in the first instance in 1930 at the rate of 2 tons/acre and subsequently every five years:

Percentage composition of sward (based on tiller numbers)

	Original sward			
	1930	1938	1946	1959
Molinia + *Nardus*	82½	37	20	—
Fescue	10½	61	22½	15
Agrostis (bent)	Trace	2	15	36
White clover	—	—	35	38
Lowland species	—	Trace	2	7
Other hill species	7	Trace	5½	4

In the first 8 years following the application of lime, coupled with an increased intensity of grazing, changes occurred in the relative amounts of the species originally present. During the second 8-year period sward changes involved the establishment of white clover and bent, together with small amounts of lowland species such as Yorkshire Fog, *Poa annua*, and various herbs. Since 1946 the original *Molinia* and *Nardus* components have disappeared and their place has been taken by *Agrostis*. Following such an unusually heavy application of lime the swards were severely overgrazed and under these conditions wild white clover thrived in spite of the normally incompatible *Agrostis*.

The next phase in our experiments was to apply lime and control the grazing animal. Under these conditions a more rapid change in the composition of the native sward is produced and the extent of the change is very much more pronounced. Thus a typical *Molinia/Nardus* sward at an altitude of 950′ was changed into a reasonably good lowland sward within a period of 16 years, as illustrated by the following figures :

Percentage composition of the sward (based on tiller numbers)

	Original sward			
	1930	1938	1946	1959
Molinia + *Nardus*	77	—	—	—
Fescue	17½	52	2½	5
Agrostis	½	½	2½	9
White clover	—	7	40	25
Other species	5	40½†	55†	61†

†Mainly lowland grasses and herbs such as Yorkshire Fog, annual meadow grass, rough-stalked meadow grass, and smaller amounts of perennial ryegrass, cocksfoot, timothy, crested dogstail, dandelion, plantain and daisy.

Between 1946 and 1959 the contribution of herbs on the limed plots increased markedly ; these were mainly members of the Compositae particularly dandelion and daisy.

The application of fertilisers, combined with a measure of control of the grazing animal, not only changed the botanical composition of the hill swards more rapidly and to a greater extent, but also increased the yield of herbage and improved its seasonal distribution. Investigations (*J. agric. Sci.* 53, 268—285, 1959) in conjunction with the Dept. Agric. Chem. U.C.W., showed that the application of fertilisers, particularly lime, to the upland swards improved the chemical composition of the herbage. The produce from

the limed areas give a higher liveweight gain of sheep, a higher digestibility, and a higher mineral retention compared with that from the unlimed plots.

The evidence suggests that there are levels of calcium in the herbage from the unlimed fescue and *Molinia* areas of mid-Wales which are so low that they even impair herbage utilisation by the grazing animal.

Surface seeding of hill pastures

Hitherto we have been concerned with hill pastures without the deliberate introduction of new plants by seed sowing. Experiments have shown that it is possible to establish more useful grasses and clovers by oversowing the existing swards, but this can only be accomplished on a closely grazed sward after applications of lime and phosphate.

Following the applications of lime and phosphate to the native sward, and the consequent increased intensity of grazing, a fair measure of establishment of ryegrass, crested dogstail and white clover was obtained when the seed was broadcast 12–18 months after the fertilisers. These sown species, however, failed to develop into the main sward constituents because of competition from native species such as bent or fescue, or because of severe over-grazing. It was noticeable that over-grazing caused a rapid disappearance of the *Nardus* and *Molinia*, but it also seriously retarded the development of some of the sown species. In one *Nardus* sward the sudden disappearance of the *Nardus*, coupled with the failure of the sown grasses to persist on account of the severe over-grazing, resulted in a thin sward of grass and clover with a dense cover of moss. Attempts to improve bent/fescue swards on this pattern have generally resulted in an increase in the bent and a decrease in the fescue. On account of the aggressiveness of the bent, the maintenance of an abundance of clover in such a sward necessitates close grazing during mid-summer.

Reseeding of hill land

There is no doubt that considerable improvement of hill land can be effected without the introduction of more useful species by sowing, but this is a gradual process over a period of several years. To effect an immediate improvement which goes beyond the level which can be achieved by other means, it is necessary to introduce,

by sowing, an effective legume and more useful varieties of grass. Drastic surface cultivation has been shown to provide a very satisfactory seed bed for the establishment and development of the seedlings, but owing to the incomplete kill of the native herbage the results are often disappointing due to the gradual regeneration of the native species, particularly under inferior management.

Experiments involving cultivation by ploughing have shown that very often the initial take of seed is less good than after surface cultivation, but the ultimate sward, with correct management, can remain stable over many years. A large number of grass varieties have been sown on ploughed hill land, and of these S.23 perennial ryegrass has so far proved to be the most successful. Ten years after reseeding, swards based on S.23 and wild white clover still consist of about 70% of the sown species. S.23 retards the re-entry of the native species and when included in more complex mixtures on these hills, which are normally subjected to hard grazing by sheep, it assumes a dominant position in the sward within two or three years. Most varieties of perennial ryegrass give a better performance than cocksfoot and timothy under these conditions. Amongst the cocksfoots, S.143 has given the best results but under a high intensity of sheep grazing, and particularly hard grazing in the spring, it is generally inferior to ryegrass. The hexaploid timothies have also proved disappointing, and their contribution to the sward after about five years is negligible. The diploid S.50 timothy, however, stands up to hard grazing and provides green herbage during the winter, but although it can successfully withstand continuous hard grazing it cannot prevent the re-entry of the native species as effectively as the S.23. Bent seed was not included in any of the seeds mixtures but many areas have reverted to bent following the disappearance of the less suitable sown species. Compared with S.23 these bent swards are generally deficient in white clover and the autumn grown herbage suffers far more from winter burn.

The effect of hill pasture improvement on sheep

Attempts have been made to evaluate the sheep production on native hill swards in comparison with adjoining areas which were improved by reseeding (Plate 2). The following figures give some of the data on lamb production over a period of 14 years on a trial conducted on hill land at an altitude of 1,250′. One of the reseeded swards was based on the ordinary varieties of grasses, and the other on Station-bred varieties.

	Native hill pasture	*Improved hill pasture sown with*	
	Unimproved	*Ordinary grasses*	*Station-bred grasses*
Number of lambs reared per acre	17	36	40
,, ,, ,, ,, ,, 100 ewes	83	106	110
Average weight per lamb (singles)	42 lb.	52 lb.	54 lb.
,, grading† ,, ,,	$5\frac{1}{2}$	$6\frac{3}{4}$	$7\frac{1}{4}$
,, value ,, ,,	46/-	61/-	66/-
Average annual value of lamb produced per ewe	38/-	65/-	73/-
Total weight of lamb produced per acre	715 lb.	1768 lb.	2002 lb.
Total approximate value of lamb produced per acre	£40	£108	£124

†Grading scale (to indicate condition of lamb)

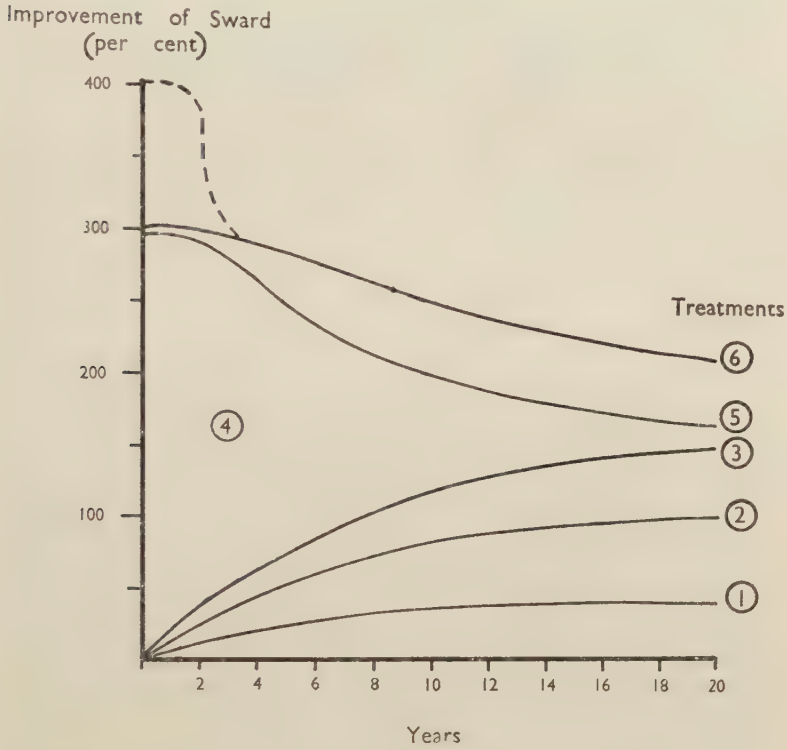
10 — prime fat
8 — fat
6 — store condition
4 — poor stores

Owing to lack of shelter on the experimental areas no sheep were maintained on any plots after the second week in January, but the time of their withdrawal varied according to the amount of herbage available. In all cases the sheep were normally returned to the hills during the second week of April just prior to lambing. The average dates of withdrawal from the plots are shown by the following :

	Unimproved sward	*Improved swards*
Ewe lambs	1st week September	3rd week November
Ewes	3rd week November	2nd week January

Thus the period of wintering away from their respective pastures, and consequently the cost of wintering per sheep, was considerably greater for those grazing the unimproved pastures. When this is considered in conjunction with the value of lamb produced per ewe, it is obvious that a far greater margin of profit is obtained by wintering the higher-producing sheep from the improved areas for a shorter period, than the lower-producing sheep from the unimproved swards for a longer period.

Levels of improvement expected in hill swards over a period of 20 years after various treatments



Treatments

1. Influence of controlled grazing
2. Effect of the application of lime and fertilisers
3. Combination of treatments 1 and 2
4. Would represent treatment 3 plus surface sowing of seeds, but graphical representation is difficult because the degree of improvement depends on the nature of the original sward. Thus for a dense bent/fescue sward the improvement would not be much better than for treatment 3 ; for heather it approaches that of treatment 5, whereas in *Molinia* and *Nardus* swards the improvement lies between these extremes.
5. Effect of surface cultivation and seed sowing in combination with treatment 3.
6. Same as 5, but cultivation involves ploughing which results in a complete kill of native herbage. The broken part of the curve represents improvement associated with the growing of pioneer crops (rape and/or turnips) before reseeding.

SEED MULTIPLICATION

Gwilym Evans

PRODUCTION AND DISTRIBUTION OF FOUNDATION SEED (H.M.R.)

The production of first generation seed by clonal propagation was continued for established and potential varieties of herbage plants with the planting of four areas (2½ acres) and the harvesting of 13 crops (7 acres) during the current year. To produce Foundation Seed of ryegrass and clover varieties on a field scale 80 acres (11 crops) were sown and 142 acres (14 crops) were harvested in 1959.

Foundation Seed of grass and clover varieties was distributed during 1958/59 to farmers for sowing 804 acres for the production of Stock Seed on contract with the N.I.A.B. Cambridge. This acreage is somewhat higher than the 689 acres sown the previous year, but it includes companion seed in addition to the main crops, whereas in 1957/58 no clover seed was available for use as companion to the grass varieties. In addition, 3 tons of S.22 Italian ryegrass were allocated for further multiplication in Northern Ireland under the auspices of their Ministry of Agriculture. Following the distribution of Foundation Seed in Spring 1959 the reserves of clover seed, especially S.184 white clover and S.151 red clover, became very low. To safeguard future supplies advantage is to be taken of the large yields of very high quality seed harvested in 1959, and it is hoped to be able to maintain a reserve bank eight times the average annual requirements of each clover variety, instead of four times as formerly.

A total of 76 tons (135 lots) of oat varieties bred at the Station was distributed in 1958/59 to seed merchants and associations operating approved Cereal Seed Crop Inspection Schemes. Oat stocks of potential varieties were also distributed for trial purposes. Included in the Foundation Seed distribution was a first release of 335 cwt. of the new winter oat variety Penrhyn S.234. A small acreage of the mildew-resistant spring oat variety Manod S.235 was also sown in 1959 with a view to releasing it to the trade in 1960.

The year 1959 will undoubtedly be remembered by the seed industry for the very favourable harvest of clover seed, when yields of over 2 cwt./acre of white clover and 6 cwt./acre of red clover were not uncommon. The dry sunny conditions, which favoured the

production of plentiful nectar and facilitated good pollination and seed setting, reduced the amount of recovery growth to such an extent that the harvesting of white clover on the lighter soils became difficult. In many instances the seed heads were only high enough to be cut with the mower and thus were not easy to collect. This problem was largely overcome, however, by using forage harvesters for picking up the cut material or for cutting and blowing the material into wagons. With more experience of this method of harvesting, together with pre-harvest desiccation, white clover seed production could undoubtedly become much more attractive to growers.

RESULTS OF EXPERIMENTS

Seed ripening in grasses (G.E.)

The appearance of the head, and the condition of the seed at the stage of *maximum* seed yield, are of prime importance in harvesting grasses at the optimum time. Seed ripening and yield have been studied in heads of the same age relative to anthesis, and also in random samples. Some of the results are summarised on page 54 the species are given in order of heading date.

This study has shown a distinct tendency for the period between anthesis and production of maximum seed yield on an individual head to be shorter as the heading date of these species becomes later. Meadow foxtail has taken 30 days, but a *Phalaris* hybrid only 19 days. It appears that in all these grasses, and also in perennial ryegrass, the head carries the optimum weight of seed several days before it has lost all its green colouring. Similarly most of the caryopses still retain a shade of green, and it is important to observe that at this stage the endosperm has only reached the consistency of 'cream cheese,' or become 'cheesy.' As traces of green disappear and the endosperm hardens the seeds are liable to shatter and thus reduce the yield per head.

The above observations apply to heads conforming to the same stage of development, but random samples consist of heads at different stages. The range of ripeness depends on the genetic constitution and on the prevailing weather conditions. Two or more peaks of anthesis may provide a plateau extending over a week or more at maximum yield allowing a convenient latitude for harvesting. As the earlier ripening seeds shatter the later ones increase in weight to compensate. On the other hand, when there

Species and variety	*Days from peak anthesis to maximum yield*	*Appearance of majority of heads*	*Condition of seed on head*	*Caryopsis*	*Consistency of endosperm*
Meadow foxtail S.55	30	Grey. Greenish tinge	Most strip easily at top	Greenish-yellow to yellow	'Cream cheese' to 'cheese'
Cocksfoot S.37	26	Yellowish-brown. Greenish tinge	Strip easily at top. Yellowish-brown. Green tips	Green to yellow-green	'Cream cheese'
Cocksfoot S.143	26	Brownish-yellow. Distinctly greenish tinge	Strip fairly easily. Green tinge	Greenish-yellow	'Cream cheese'
Meadow fescue S.53	22	Yellowish-brown with green or purple tinge	Most strip easily. Yellowish-green or yellowish-purple	Green	'Cheesy'
Phalaris hybrid S.230	19	Greenish-yellow	Stripping not easy. Yellowish-green, shiny, some grey	Green	'Cheesy'

is only one distinct peak of anthesis there appears to be a corresponding peak of maximum yield ; a delay in harvesting for the few days following that peak may cause substantial loss through shattering.

The effect of sowing rates and nutrition on seed yields (G.E.)

The harmful effect of excessive seed rates on seed yield has persisted into the third harvest year (1959) for tall fescue S.170, meadow fescue S.53, cocksfoot S.37 and *Phalaris* hybrid S.230 when a spring application of nitrogen was *withheld*. A clear downward gradient was shown as the seed rate was increased, but it was less steep than in previous harvest years, especially in cocksfoot. Plants of these four species spaced 1′ apart have given superior seed yields over drills sown at various rates, even in the third harvest year. On the other hand, drills of perennial ryegrass (S.24) have out-yielded in three successive harvest years gapped drills and spaced plants.

With applications of nitrogen the seed rate effect has disappeared by the third harvest year in cocksfoot, meadow fescue, perennial ryegrass and *Phalaris*, but a significant difference has persisted between the yield of spaced plants and the thick sowing of tall fescue. These results indicate that under conditions of high fertility the yields from a range of rates become levelled in the later harvest years.

A strong contrast obtains in the reactions of seed yield to seed rate in the various species. Adjustment to the highest density is greatest in perennial ryegrass, and least in tall fescue, but the reverse is true for the lowest density.

After an application of NPK in the autumn, *Phalaris* shows the greatest response to spring nitrogen and tall fescue the least. Thus it seems that much greater attention is required for the manuring and management of tall fescue in the autumn.

The effect of defoliation (G.E.)

It was shown in an experiment in 1937 (*Welsh J. Agric.*, 13, 195–211, 1937) that the pasture variety of perennial ryegrass S.23 endured grazing in early spring without detriment to seed yield when NPK fertiliser was applied about the same time as the grazing. In the experiment now completed, hard cutting in the autumn of the sowing year of the early type of perennial ryegrass S.24 reduced seed yield, but nitrogen applied as late as anthesis corrected this disability.

Autumn cutting of S.24 before the second and third harvest years increased seed yield when NPK fertiliser was applied at the time of defoliation. Whereas after summer sowing an abundance of young shoots is produced by autumn with sufficient hardiness to withstand the rigours of winter, mature stands have many old shoots by autumn after a seed harvest. Thus autumn defoliation, coupled with manuring, invigorates an old stand by removing the old shoots and induces the development of young shoots capable of over-wintering and producing strong seed heads next spring.

In another experiment S.143 cocksfoot produced a greater seed yield as the result of defoliation at the beginning of heading in the previous year (1958). This reaction confirms data already obtained on S.26 cocksfoot, and shows that when the seed yield is reduced under certain conditions there is at least some compensation in the yield of the next year's crops.

The effect of a cereal cover crop on the seed yield of grass varieties (H.M.R.)

Previous results (*W.P.B.S. Rep.* 1950–56, p. 147, 1958) indicated that as a consequence of undersowing with barley the seed yield of cocksfoot S.26 and tall fescue S.170 was only 32% and 34% respectively of that of the control, but timothy S.51, perennial ryegrass S.24 and bent Br.616 each gave 78%, 83% and 100% respectively of control yield.

This differential response in terms of seed yield to undersowing is probably linked with the capacity of the species to tiller under shaded conditions, and/or to form new tillers immediately after the removal of the cereal nurse crop, and/or to tiller under colder soil conditions in the autumn/winter period. In practice very similar reactions have been observed when these species were sown late in the year. Cocksfoot and tall fescue seed crops sown after July cannot reasonably be expected to produce a high seed yield the following year, whereas both perennial and Italian ryegrasses sown in September or early October have on most occasions given satisfactory yields of seed.

Following this initial investigation it was decided to study the problem further, using S.26 cocksfoot which in the earlier trial proved to be the most sensitive to the depressing effect of the cover crop.

The seed was sown in 2′ 6″ drills at 4 lb./acre (1) without a cover crop, (2) with full cover crop of oats, and (3) with partial

cover crop, obtained by blocking one corn drill in five (drills 6″ apart) and sowing the cocksfoot seed in the blocked drill.

In addition treatments 2 and 3 received differential dressings of N to study the effect of time of application on the subsequent seed yield.

The experiment concluded in 1959 covers three successive cocksfoot seed crops following the corn harvest in the seeding year. The results, summarised below, show highly significant variation due to treatments, years, and year × treatment interaction. All plots received 4 cwt./acre complete fertiliser NPK in September, and 4 cwt./acre nitro-chalk in March for three years.

	Seed yields lb./acre (nearest lb.)							
	Cover crops of oats							*L.S.D.*
Harvest year	*Control*	*Full*			*Partial*			*P = 0.05*
	A	*B*	*C*†	*D*††	*E*	*F*†	*G*††	
1st	792	407	431	543	557	619	697	95.42
2nd	313	390	350	322	357	353	301	
3rd	1056	1041	1100	1140	1106	1135	1112	
Mean	720	613	627	668	673	702	703	59.98

†Plus an extra 3 cwt./acre nitrochalk in the autumn
†† ,, ,, ,, ,, ,, ,, ,, ,, spring } 1st year only

As in the original trial, the seed yields of all treatments involving the cereal cover crop were significantly lower in the first year than those of control plot (A), but it is more important to note the mean increase of 150 lb./acre in yield as a result of blocking one corn drill in five (i.e., mean of columns E, F, G minus mean of B, C, D). The reduction in seed yield as a result of undersowing was related to a reduction in the number of inflorescences, and also in the amount of seed per panicle. The extra application of N in the autumn produced more inflorescences, and the extra spring dressing appeared to increase the weight of seed per panicle.

Although the mean seed yield was generally much lower in the second harvest year, with no significant variation between yields, it is interesting to note that the highest yielding plots in the first year (columns A and G) gave the lowest yield in the second year; treatment B, which gave a very low yield in the first year, produced more seed than the other six treatments in the second. Third harvest year yields, which were at a high level throughout, were remarkably similar for all six treatments.

It would appear, therefore, that with the liberal use of autumn and spring nitrogen reasonable seed yields can be obtained from drill crops of cocksfoot over a period of three successive harvest years,

even when they have been established under a cereal cover crop. Better yields, however, are obtained in the absence of a cereal, but when it is absolutely essential to grow a cereal cover crop the depressing effect can be partly eliminated by blocking one spout in three or four of the cereal drill.

Effects of gibberellic acid on herbage legumes (J.L.S.)

An experiment over the last two years to study the influence of growth stage on the response of S.123 extra-late flowering red clover (*Trifolium pratense* L.) to applied gibberellic acid (G.A.) was completed during the summer (1959). A total of 25 combinations of spraying frequency and growth stage was studied on single plants.

All treatments induced earlier flowering, the maximum effect being noted in plants receiving three sprayings, and the least in those which had only one.

In order to increase the number of heads per stem it was necessary to spray two or three times during the extension of the first four internodes, followed by a single treatment at the eighth or tenth. Such a treatment pattern ensures that the first formed internodes and the secondary branches, both of which are comparatively slow in extension, complete their active growth phase in a much shorter time. This in turn means that the process of heading is accelerated and more branches come to fruition.

In all treated groups there was a very large increase in multiple heading, that is, the production of more than one head in each leaf axil, and this too made a significant contribution to the observed increases in head production on a per-stem basis.

Control plants produced a mean of 292.95 heads per plant whilst the best treatment groups at harvest produced a mean of 444.50 heads.

If these techniques can be translated into field practice real increases in potential seed yield per acre will be obtained. Work on this aspect is already in progress.

The physiology of growth habit and flowering in herbage legumes (J.L.S.)

A comprehensive study of the physiology of flowering and growth habit of red clover varieties is in progress. Initial work has been concerned with factors influencing stem and internode development, as well as with seedling characters of importance in varietal identification.

Stem production was markedly affected by photoperiod, and thus plants exposed to short day conditions for several months before being induced to head produced four times as many stems as those grown throughout under long days. In all treatments it was possible to demonstrate a significant difference between early and late varieties in terms of the number of stems produced, but the difference was only just significant in long-day treated material. It was not possible to distinguish varieties within each group on the basis of number of stems.

The number of elongated internodes per stem is a useful character in distinguishing red clover varieties, as Williams (*Bull. Welsh Pl. Breed. Sta.* Ser. H. No. 7, p. 17, 1937) and Hawkins (*J. Brit. Grassl. Soc.* 8, 213–233, 1953) have shown, but it now appears that this is only of use in dealing with short-day treatment material, i.e., first harvest year plants. When the number of elongated internodes per stem is considered, late-flowering varieties grown under continuous long days do not differ significantly from early-flowering types grown under the same conditions. Such plants would be equivalent to stands in the year of sowing.

A high correlation ($r = +0.729$, $P = 0.01$) has been established in uncut material in the first harvest year between the number of tillers in the basal rosette at the advent of critical daylength and the number of stems produced at full bloom, provided no cutting treatment is imposed upon the plant. Thus there is a possibility of selecting for head production on the basis of rate of tillering in the seedling plant, for it has already been established that the number of heads/plant has a close and obligatory connection with the number of stems.

Seedling growth habit at the sixth leaf stage, and also simple leaf area, appear to be useful characters in differentiating between red clover varieties.

Seed yield of late-flowering red clover (J.L.S.)

The normal management practice for seed production in late-flowering red clover is to control flowering by grazing or cutting up to about 1 June, the object being to synchronise maximum flower production with the peak population of wild bees. It was felt that climatic factors might influence the build-up of the bee population and in a favourable year such as 1959 it would be an advantage to have maximum flower production earlier in the year. This suggestion was substantiated by an experiment in which normal cutting manage-

ment was compared with a naturally-flowering crop. Consistently higher yields were obtained when the crop was not cut or grazed. The mean yield of clean seed following cutting was 3.7 cwt./acre with a maximum of 3.9 cwt., while uncut or ungrazed crops gave a mean of 7.9 cwt./acre with a maximum of 10.7 cwt. In assessing the value of these results it must, however, be borne in mind that recovery after cutting in a dry year is less satisfactory and also that harvesting problems associated with excess leafage in uncut herbage also arise.

The influence of water table, soil depth and soil type on the survival of certain crop and weed seeds (J.L.)

Rapid depletion of seed numbers in loam soil, sand and peat up to a maximum depth of 8″ was found to be mainly attributable to germination *in situ*. Seeds below the water table remained dormant and highly viable after two months, whereas those above the water table had germinated freely and consequently soon perished. The species differed in their reaction to the three soils, but from the results it is clear that type of soil as such had only little influence on seed survival.

PLANT PATHOLOGY

A. J. H. Carr

Clover virus diseases

Two virus yellows (jassid-transmitted) diseases are known to affect clover (Frazier, N. W. and Posnette, A. F. *Ann. appl. Biol.* 45, 580–588, 1957), phyllody, which causes vegetative proliferation of the flower head thereby reducing seed setting, and witches' broom, which causes crowding of the axillae giving a characteristic brooming effect accompanied by marked chlorosis and clubbing of the younger leaves. Symptoms of phyllody have been observed on white clover for many years, but recently there are indications of a probable increase in the frequency of this disease. In the Legume Breeding Nurseries Mr. W. Ellis Davies reports a third condition, provisionally termed 'red leaf' because of leaf bronzing which accompanies a general reduction in vigour, and is probably also of virus yellows origin. 'Red leaf' affects plant vigour much more severely than phyllody, infected plants weigh 20%–40% less than healthy plants, and often fail to survive the winter. Symptoms normally first observed in the field in mid-April become more severe under drought conditions. Recovery growth is slow, the leaves being small, yellowish-green, and sometimes red. Flowers are normal, and plants showing symptoms have relatively less phyllody than those unaffected by 'red leaf.'

The following data, taken from the Legume Breeding records, show clearly the increase in the incidence of phyllody on spaced plants of white clover at the Welsh Plant Breeding Station in recent years :

Percentage of infected plants of white clover, 1956–1959

First bloom				*Aftermath bloom*		
1956	1957	1958	1959	1957	1958	1959
2.8	6.5	11.8	13.7	25.7	22.2	26.0

The data are from a continually changing plant population, and the figures for first bloom (representing primary infection) may be taken to indicate an overall increase in disease potential, rather than a build-up of the virus within a static population. The figures recorded for the aftermath bloom illustrate the degree to which phyllody can become prevalent in a population due to secondary

spread, and possibly do not show the same increase in successive years due to the equilibrium point being reached.

As a result of these observations, and in response to a request from the N.A.A.S. Grassland Officers whose experiences had been similar, two surveys on the incidence of the disease in white clover seed crops were undertaken in 1959 ; a general survey by N.A.A.S. seed inspectors, covering 296 crops (S.100, S.184 and Kersey white clovers) and a smaller survey, by the writer, of 23 crops chosen at random in East Anglia, the region in which half of all white clover seed crops are grown. The disease was recorded as absent, occasional, frequent or severe, and the smaller survey also attempted to ascribe to each crop a percentage for flower heads showing symptoms, as well as recording data for ' red leaf ' and witches' broom.

The general survey showed that phyllody was present in 40% of the crops, reaching frequent or severe proportions in 5%. A comparison of the inspectors' data with those of the pathologist for the 23 crops in East Anglia, which had been examined by both, revealed that frequently a lower assessment of disease incidence was made by the inspectors. For this reason, the overall incidence of phyllody may well be higher than the general survey indicated.

Phyllody was present in all 23 crops examined in the East Anglia survey, being occasional in 13, frequent in 9, and severe in 1. A figure of 14% recorded for the severely infected crop serves to underline the potentially high level to which this disease is capable of building up in a white clover stand, and at this frequency would almost certainly have an adverse influence on the seed yield.

There was very little evidence of zonation in the distribution of the virus, except in Lincolnshire and Nottinghamshire, where phyllody appeared to be somewhat less prevalent. It was apparent also that the incidence was somewhat lower in areas where white clover seed production was less intense, being present in only 26% of these crops as opposed to 44% of crops in intensive areas. The finding of an area with a low incidence of phyllody is highly desirable for the strawberry grower, for the isolation of stocks free from the risk of infection by green petal disease (caused by the phyllody virus) from nearby infected white clover plants.

One clear result of the surveys was that phyllody increases with increasing age of stand, both in the likelihood of a crop becoming infected, and in the overall incidence within a crop. Thus, phyllody was present in 33% of first year stands, and in 46% of those in their second or third harvest year, while the East Anglia survey showed an increase in mean frequency within crops from 0.47% flower

heads showing symptoms to 2.76%. No definite conclusions could be drawn as to the relative susceptibility of different white clover varieties, but disease incidence was generally lower in S.184 than in either of the larger leaved varieties.

Inspectors were asked to record any virus diseases found in red clover crops, but only two reports of phyllody in this species were received, and it would appear that at present the virus is not a serious problem in red clover in the field, although it can be transmitted readily in the glasshouse from white clover to red clover.

'Red leaf' was present in all but one of the 23 crops examined in East Anglia, and witches' broom in 7. It may well be that when more evidence is available as to the effect of these diseases on the productivity of a sward it will be found that they are no less important than phyllody.

The overall implications of these surveys are that phyllody virus is widely distributed in white clover seed crops and can, on occasions, reach proportions where seed yield would be expected to be reduced. Furthermore, they demonstrate the need for continued research on the effect of all three diseases, on vector control, and on the possibility of breeding resistant lines.

A further experiment has been conducted by Mr. W. Ellis Davies in conjunction with the Advisory Entomologist and Advisory Pathologist, N.A.A.S. (Wales), Trawscoed, in an attempt to control the leaf hoppers responsible for the spread of the phyllody virus (*Euscelis* and *Macrosteles* spp.). The spray materials DDT/BHC and Demeton Methyl were used fortnightly at appropriate times. One set of plots received the DDT/BHC twice in the autumn and twice in the spring.

Insect traps were set up to measure leaf hopper activity. This was small in mid-September 1958 and spring 1959, but in July 1959 the counts increased and reached a peak at the end of August.

The number of plants affected with phyllody was small when assessed in June and August 1959, but increased to 18% at the beginning of October. There were no differences in the number of plants showing virus symptoms, or in jassid counts, which could be ascribed to spraying treatments. It is now thought that the plots, which measured 20 × 5 yds., were too small for this experiment.

Cocksfoot streak virus

This virus disease, first recorded in 1950 (Smith, K.M. *Plant Pathol.* 1, p.118, 1952), is now widespread. Little is known about

its transmission and effects, although the disease may be transmitted, with difficulty, by sap inoculation. Using this method, marked differences in susceptibility among cocksfoot genotypes have been found.

The effects of this disease are being studied by Dr. Ellis Griffiths and Mr. P. L. Catherall, Dept. Agric. Bot., U.C.W., on single plants in pots and in simulated swards with known proportions of healthy and infected plants.

The single plant studies comparing healthy and infected plants of the same genotype have shown that infected plants tiller less, have a reduced response to fertiliser application, particularly nitrogen, and recover more slowly from cutting.

In simulated swards cut at monthly intervals it was found that swards with 100% healthy plants outyielded by 60% those with 100% infected plants. Swards with equal numbers of healthy and infected plants gave yields better than intermediate, and there is evidence that this was due to the more vigorous growth of healthy plants under these conditions.

In the Grass Breeding Nursery some mature plants of *Dactylis glomerata* severely infected by the streak virus were selected by Dr. Slykhuis† from amongst the large population of spaced material. Mr. Beddows reports that the progeny from nine of the most severely infected plants which had been allowed to interpollinate were kept under observation in the Nursery during 1957–1959, but they failed to develop virus symptoms. It would appear, therefore, that in cocksfoot (as in strawberry) the virus is not seed transmitted.

Verticillium wilt of lucerne

This disease is of comparatively recent origin in Britain, but is already widespread and destructive, and represents a serious hazard both to the continued cultivation of lucerne in areas where the crop is established in agricultural practice, and also to its introduction as a desirable nitrogenous crop in other areas. Two serious drawbacks of this disease are the difficulty of applying control measures, and the fact that so far all cultivated varieties tested have proved to be susceptible. There is, however, a wealth of wild *Medicago* spp. available (many intercrossing with *M. sativa*) within which to search for resistant material.

Nine seed collections, representing 6 distinct species and one natural *M. sativa* × *M. falcata* hybrid collected in Ayrshire, were

† Then working in Dep. Plant Path., Rothamsted Expt. Sta.

tested for *Verticillium* wilt resistance by the method of Isaac (*Ann. appl. Biol.* 45, 550–558, 1957). Plants were scored as having no symptoms, slight, moderate or severe infection.

Results obtained from infecting Medicago *spp. with* Verticillium *wilt*

	No. tested	*Percentage plants in each class*			
		Absent	*Slight*	*Moderate*	*Severe*
Medicago sativa (var. Du Puits)	30	0.0	10.0	26.7	63.3
M. falcata (diploid)	12	8.3	58.4	33.3	0.0
M. ,, (tetraploid)	10	0.0	40.0	30.0	30.0
M. sativa × *M. falcata*	10	80.0	20.0	0.0	0.0
M. gaetula (No. 751)	30	13.3	30.0	46.7	10.0
M. ,, (No. 753)	10	30.0	30.0	40.0	0.0
M. platycarpa	20	0.0	10.0	0.0	90.0
M. glutinosa	10	20.0	10.0	60.0	10.0
M. caerulea	6	33.3	16.7	33.3	16.7
	138	14.5	23.2	29.7	32.6

Although the small and irregular numbers of seed available made a completely statistical lay-out and analysis impossible, the figures show that there were considerable differences between the species tested (and even between different samples of the same species) in the proportion of resistant plants. All species except *M. platycarpa* were better in this respect than Du Puits, the control variety of *M. sativa*. The natural *M. sativa* × *M. falcata* hybrid was the most resistant, and as *M. sativa* has very few resistant genotypes it would appear that the resistance of the hybrid was attributable to the *falcata* parent. On cytological examination the hybrid was found to be tetraploid, and thus it is surprising that of the two samples of *M. falcata* tested, the diploid material was more resistant than the tetraploid. It is concluded that different races of *M. falcata* may differ in their resistance to *Verticillium*, but that these differences are not correlated with ploidy.

These results demonstrate the need to include several population samples of a species in testing for disease resistance, and emphasise the necessity of testing large numbers of plants in order to obtain sufficient desirable genotypes which may exist only in low frequency in a population. In this respect the aims of the plant breeder are somewhat different from those of the pathologist, the latter being more generally concerned with the frequency of resistant genotypes in a variety to assess its *ad hoc* usefulness in an area where the disease is prevalent. Although at this stage any conclusions must be tentative, it would appear that a breeding programme which attempts

to combine the resistance of certain genotypes of *M. falcata* with the agronomic type and productivity of *M. sativa* offers a reasonable chance of success.

' Stunting ' in *Lolium perenne* (A.R.B., D.E.S.)

In the Grass Breeding Nursery during the summer of 1955 a number of plants of *Lolium perenne* became stunted. The condition spread rather alarmingly, resulting in the death of many of the clones. Leaves of affected plants lost their chlorophyll, became brown and shrivelled. The condition was largely confined to perennial ryegrass. On examination by the Advisory Mycologist and Advisory Entomologist, N.A.A.S. (Wales), Trawscoed, Take-all and Stem base rot (*Ophiobolus* spp.), Black root-rot (*Thielaviopsis* sp.) and Root-rot (*Rhizoctonia* sp.) were found, as well as eelworms (*Panagrolainus* sp. and *Ditylenchus dipsaci*). The numbers of the parasitic *Ditylenchus* were low, but for the saprophytic *Panagrolainus* they were relatively high.

The control of eelworm

Although it appeared that the population of *D. dipsaci* was too small to be the primary cause of ' stunting ', it was considered desirable to achieve some measure of control. Since basic stocks of breeding material are rejuvenated by clonal propagation, the use of hot water treatment as for tulips and chrysanthemums suggested itself, and trials utilising hot water and a 5% solution of parathion as treatments were initiated in collaboration with the N.A.A.S. Unfortunately, treatment of single tillers in water at 105°, 107° and 110°F. for 5, 15 and 30 minutes gave no significant reduction in the numbers of eelworms, and since a pilot experiment showed that an immersion time of 120 minutes killed the plants at all three temperatures the method would not appear to offer a great deal of promise. In the experiments with parathion, single tillers were dipped in the aqueous solution prior to planting, and the leaves sprayed a fortnight later, the spraying treatment being repeated three times. In the initial experiments, some degree of success appeared to have been achieved, the treated tillers making excellent growth while the untreated remained stunted, but these results were not obtained in repeat experiments, although the parathion itself had no deleterious effect.

The control of the fungi

The various chemical treatments used in an attempt to effect control of *Ophiobolus*, *Thielaviopsis* and *Rhizoctonia* were :

Pure phenol		2 g.	in 500 ml. water
,,		5 ,,	,,
,,		10 ,,	,,
Aretan:	Mercurial compound	2 ,,	,,
,,	,,	10 ,,	,,
Jeyes fluid:	25% mixed phenols	10 ml.	,,
	,,	20 ,,	,,

Phenol at 5 and 10 g./500 ml. and Aretan at 10 g. proved lethal to the plants. Of the remaining treatments those utilising Jeyes fluid allowed gradual recovery of the treated tillers, and similar effects have been noted in subsequent tests in the field. The treatment with Jeyes seems to allow any disease-free tillers present to make active growth, but recovery has not always been complete.

As a result of these experiments, a standard technique has been adopted. The healthiest tillers are washed in water, allowed to stand in 2% Jeyes fluid for two minutes, re-washed after draining and then planted in sterilised soil. If poor growth still results the treatment is repeated. In this way it is hoped to build up a museum of clean plants.

CHEMISTRY

G. ap Griffith

Routine analytical work for other sections again showed an increase. The number of Kjeldahl determinations alone exceeded 12,000, in addition to 150 mineral analyses of herbage, nearly 300 dungs and urines and a number of miscellaneous analyses. Some reduction would be effected by the bulking of replicates where the nitrogen content of the herbage was of secondary importance, and an investigation was planned to study the statistical implications of this.

Some of the work on nitrate accumulation in herbage is reported in a separate article on p. 94.

CYTOLOGY

KEITH JONES

The cytological survey of F.A.O. collections of *Dactylis* spp., has been completed, and a list of chromosome numbers is available to research workers who are interested in this material. The collections contain both diploid and tetraploid plants, but of special interest is our discovery that F.A.O. Lot No. 3076 from Cyrenaica was hexaploid ; it is the first naturally-occurring material to be recorded with this number. Preliminary analyses of meiosis show that chromosome pairing is regular, and although quadrivalents, sexivalents and some higher multivalents occur, in most metaphases univalents are rare. Multivalent frequency is not high, and there is every indication that the plants will be of good fertility.

Chromosome counts have been made of 17 collections (55 plants) of *Agropyron repens* kindly sent from various parts of England and Wales by officers of the N.A.A.S. All plants have been found to be hexaploid ($2n = 42$).

The statistical analyses of the randomised block lay-out designed to compare the morphology of 4x, 5x and 6x *Holcus mollis* are almost complete. The results confirm that none of the numerous characters measured can be used to separate the chromosome races in the field. Despite appreciable genetic discontinuity therefore they must continue to be included in a single taxon. There is further evidence to indicate that the pentaploid is of hybrid origin.

Similar analyses made on plants of *H. lanatus* ($2n = 14$), *H. mollis* ($2n = 28$) and different F_1 hybrids between them, show the hybrids to be identical with *H. mollis* in floral characters. The measurement of intermediacy in other characters may enable certain hybrids to be recognised in the field.

PENNANT S.227 — A NEW VARIETY OF WINTER OATS

Breeding history

Stem eelworm resistant variety developed from the same cross as Powys, namely S.172 × S.147 made at the Welsh Plant Breeding Station in 1940. First isolated as a promising eelworm resistant segregate in 1952 and after further re-selection and re-testing for resistance it was submitted for official yield trials under Station No. W.271.

Agronomic features

In W.P.B.S. and N.I.A.B. official trials over several seasons, Pennant S.227 proved superior to S.147 in yielding ability and standing power, its straw being stiffer and approximately 6″ shorter. In winter hardiness, tillering capacity and general panicle characteristics it closely resembles its sister variety Powys but produces a grain sample approaching that of S.147 in size, plumpness and milling quality. Pennant matures slightly earlier than S.147 and is intended for growing on soils of moderate to good fertility ; it is especially recommended in place of S.147, Penrhyn and Powys on stem eelworm infested land.

Descriptive features

Panicle open, equilateral, of similar conformation to S.147 but slightly more compact, and there is a tendency for the panicle branches to ascend at a somewhat more acute angle to the rachis than either S.147 or Powys. Spikelets two-grained. Mature grains white, medium size, plump, with a few hairs of variable length at the base of the lower grain ; very infrequently awned but an occasional fine hair usually found on the rachilla.

Husk	= 23.0% to 25.0%
Weight/1,000 grains	= 36 to 39 grammes

MANOD S.235 — A NEW VARIETY OF SPRING OATS

Breeding history

Of composite origin, derived from the following series of convergent crosses with intervening selection and re-selection designed to incorporate resistance to both mildew and crown rust into a single adapted genotype.

Victory × Red Algerian : Red Algerian × Scotch Potato

Station Sel. No. 30 Cn/1/1/14/437 × Record

Station Sel. No. 249 Cn/1/350/1 × Station Sel. No. 991 Cn/3/12

Station Sel. No. O1750/11 × Tama (crown rust resistant)
(mildew resistant)

4757/18/2/19 = **MANOD S.235**

Disease reaction

Exhibits a high degree of resistance to stem eelworm (*Ditylenchus dipsaci*), mildew (*Erysiphe graminis avenae*) and crown rust (*Puccinia coronata*).

Agronomic features

On account of its capacity to withstand mildew attacks this spring variety is specially recommended for those areas which experience regularly a high incidence of this widespread disease. Under such conditions it has shown a decided superiority over other established varieties in yielding capacity and in lodging resistance. In general yielding capacity under relatively disease-free conditions Manod is equal to Sun II, and slightly earlier in ripening. It produces clean medium-length straw of superior standing ability to Sun II.

Descriptive features

Panicle open, equilateral but tending to acquire a semi-equilateral appearance on reaching maturity. Spikelets two-grained, three-grained spikelets rare ; occasional weak awn. Grain white to creamy-white in colour, medium size ; occasional fine medium length hair on base of first grain ; rachilla glabrous ; inner palea of grain sometimes tinged light brown.

Husk = 24% to 26%
Weight/1,000 grains = 34 to 37 grammes

SELECTION FOR LEAF AREA IN RYEGRASS

J. P. Cooper and K. J. R. Edwards†

The importance of leaf area in crop plants has been recognised for several years, and is of particular significance in herbage crops where the economic yield consists of leaves, and where competition for light is operative throughout the life of the crop (Donald and Black, 1958). The ultimate efficiency of a pasture may well be expressed as the proportion of the incoming light energy utilised by the sward ; this will depend on the area of photosynthetic tissue exposed for the interception of light and also on the photosynthetic efficiency per unit area of leaf, usually measured as the net assimilation rate.

Watson (1956) has shown in several annual field crops that although seasonal and varietal differences in net assimilation rate do occur, differences in dry matter yield are based largely on changes in leaf area index, that is, the area of leaf per unit area of land. This is also true for ryegrass varieties during the seedling stage (Cooper, unpublished).

Selection for the rapid attainment of optimum leaf area, especially after defoliation, might therefore prove a useful approach to the problem of breeding for yield in the herbage grasses. Genetic studies on date of ear emergence in ryegrass (Cooper, 1959 a,b,) have revealed considerable additive genetic variation within each variety, resulting in immediate response to selection, and also great heterozygosity of parents, providing a gradual release of variation over several generations.

Such a genetic structure suggests that similar variation might be expected for the components of leaf area, giving useful response to selection either between or within varieties. It was decided therefore to study the genetic control of leaf size and rate of leaf appearance in the seedling stage. This work is being extended to the performance of older plants growing under conditions of competition and defoliation.

Three contrasting varieties were studied, Irish and Hunsballe perennial ryegrass (commercial hay variety and bred pasture variety respectively) and Italian ryegrass. The characters measured were the length, width and area of the sixth leaf on the main shoot, and the time between the appearance of the fourth and seventh leaves.

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on the main shoot. Leaf area was calculated as length × width at the mid-point, which gives an error of less than 6%. Pilot studies had shown that both leaf size and rate of leaf appearance were highly correlated on different tillers of the same plant, and that the size of successive leaves on the main shoot was also correlated.

Genetic variation

The first step was to estimate the amount of genetic variation within each variety since this provides the raw material for selection.

The additive genetic variation, i.e., that which is fixable by selection, can be assessed only from a progeny test. In the present case, pair-crosses were made between parents within each variety and the heritabilities estimated in two ways, (1) from the correlation between progeny means and mid-parent values, and (2) by the analysis of variance of full-sib families, corrected for assortative mating (Reeve, 1953). Both parents and progeny were grown in the glasshouse in autumn, but in different years, and the estimates from the correlation data may be influenced by genotype/environment interaction.

The figures obtained (Table 1) differ with character and variety, but the two methods of assessment present a similar picture. In Italian the estimates were encouragingly high for all characters.

Table 1. Heritability estimates for leaf characters

		From	
Character	*Variety*	*Parent/progeny correlation*	*Analysis of full-sib families*
Rate of leaf appearance	Irish	0.93	0.77
	Italian	0.86	0.73
	Hunsballe	0.30	0.57
Leaf width	Irish	0.15	0.28
	Italian	0.64	0.36
	Hunsballe	0.58	0.41
Leaf length	Irish	0.28	0.33
	Italian	0.73	0.41
	Hunsballe	−0.31	0.15
Leaf area	Irish	0.06	0.17
	Italian	0.54	0.41
	Hunsballe	0.36	0.26

In Irish, however, leaf length and width showed little additive genetic variation, and the figure for leaf area was almost zero, while in Hunsballe, a negative estimate was obtained from the correlation data for leaf length. These results suggest that selection should be immediately effective for all the characters in Italian, for leaf width and rate of leaf appearance in Hunsballe, but for rate of leaf appearance only in Irish. Considerable variation appeared within the first generation progeny in all varieties, suggesting heterozygosity of the parents for genes controlling leaf characters.

Response to selection

The actual response in some of these varieties to two generations of selection for leaf size and rate of leaf appearance is summarised in Tables 2 and 3. A high and low line were established within each variety using a ' fourway ' crossing system and selecting the extreme four plants in each generation (Cooper, 1959b).

Table 2. Selection for leaf size

	ITALIAN			*IRISH*		
		2nd Generation			*2nd Generation*	
	Original	*High*	*Low*	*Original*	*High*	*Low*
Leaf area (mm^2.)	1244	1733	808***	754	788	704 N.S.
Leaf length (mm.)	235	279	170***	200	199	182*
Leaf width (mm.)	5.2	6.2	4.7***	3.8	3.9	3.8 N.S.
Leaf appearance (days/ leaf)	6.7	8.1	6.7***	6.2	6.0	6.3 N.S.
Tiller No.	17.5	16.8	21.3**	21.4	24.4	18.2**
Dry weight/tiller (mg.)	34	42	24***	23	25	20 N.S.
Dry weight/plant (g.)	0.60	0.71	0.51*	0.49	0.62	0.36**

Significance of differences between high and low lines :

* P = 0.05 — 0.01
** P = 0.01 — 0.001
*** P < 0.001

Selection for leaf size proved most effective in Italian ryegrass where the changes in length, width and area are all highly significant by the second generation. A two-fold difference in mean leaf area has been obtained, and the extreme individuals are well outside the parental range. In Irish, however, only a small and non-significant increase in leaf area has been achieved as was expected from the low heritability of this character, although the changes in leaf length were just significant.

Selection for rate of leaf appearance was carried out only in Irish and Hunsballe ryegrass. Considerable response was obtained

in each variety, although the divergence was greater in Irish, where the extreme plants show a range of from under 4 days to over 8 days per leaf.

Table 3. *Selection for rate of leaf appearance*

	IRISH			*HUNSBALLE*		
		2nd Generation			*2nd Generation*	
	Original	*Slow*	*Rapid*	*Original*	*Slow*	*Rapid*
Leaf appearance (days/ leaf)	6.5	7.1	5.4***	6.2	6.9	6.0***
Leaf area (mm^2.)	797	942	451***	812	920	715***
Leaf length (mm.)	178	218	143***	212	219	205 N.S.
Leaf width (mm.)	3.5	4.2	3.1***	3.8	4.2	3.5***
Tiller No.	21.5	15.9	19.3*	21.0	18.3	22.5**
Dry weight/tiller (mg.)	34	32	28*	37	39	38 N.S.
Dry weight/plant (g.)	0.72	0.54	0.53 N.S.	0.75	0.71	0.83*

Significance of differences between high and low lines :

*** P = 0.05 — 0.01
** P = 0.01 — 0.001
* P < 0.001

The heritability as calculated from parent/progeny correlation, or from the analysis of full-sib families, evidently provides a good indication of the immediate response to be expected from selection, all the characters with a mean heritability of over 0.40 having changed significantly by the second generation.

There are dangers in selecting for a single character at one and the same time, as unfavourable correlated responses in other characters may occur. In the present work, for instance, selection for rapid leaf appearance has invariably resulted in smaller leaves, and vice versa ; this correlated response operates largely through changes in leaf width (Table 2). Selection for leaf size where effective, as in Italian ryegrass, also appears to lead to less rapid leaf appearance (Table 3). The correlation may well prove an obstacle to selecting for high total leaf area, and therefore high dry matter production.

Dry matter production

The changes in leaf characters brought about by selection might be expected to affect dry matter production in the seedling stage, and production results for the first cut taken at or about the eighth leaf stage, are given in Tables 2 and 3.

Selection for leaf size where effective, as in Italian ryegrass, led to a large increase in dry weight/tiller. This, however, was balanced by a smaller tiller number, possibly a result of slower leaf

appearance, so that the final dry weight was only slightly affected. In Irish, on the other hand, large changes occurred in dry weight/plant without any corresponding changes in leaf size or rate of leaf appearance.

Selection for rapid leaf appearance resulted in a higher tiller number at the first cut in both varieties, but this divergence disappeared in later cuts. In Hunsballe, no differences in dry weight/tiller or dry weight/plant were produced. In Irish, however, both selection lines are lower in dry weight/plant than the original variety, in the rapid line because of small tillers, and in the slow line because of fewer tillers.

It is evident that selection for leaf size or for rate of leaf appearance in the seedling stage did not have any regular effect on yield even at the first cut. This is due partly to an inverse correlation between leaf size and rate of leaf appearance, but also partly to independent differences in rate of tillering.

In conclusion, genetic variation for leaf size and rate of leaf appearance evidently exists within many ryegrass varieties, and can be utilised by selection. These findings give promise of similar variation and effective response to selection for more complex production characters, such as a rapid increase in total leaf area, or in dry matter production, especially after defoliation. Selection for these characters is already in progress.

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INVESTIGATIONS ON THE EFFECT OF DDT ON BARLEY

J. D. Hayes

Recent work at this Station has shown that barley reacts in a striking manner to spraying with proprietary compounds containing DDT (Hayes, 1959). Certain varieties are resistant and do not appear to be damaged at all, others are susceptible and suffer severe chlorosis after spraying, leaves stop growing, turn yellow and fail to recover, although succeeding leaves which have not come in contact with the spray continue normal growth and appear to be unharmed. Spraying at the early seedling stage and under unfavourable environmental conditions can cause wilting and even death of the plant. Over 200 varieties of barley grown in Europe and America have been classified at this Station on the basis of their reaction to spraying and a list of better known commercial varieties is given in Table 1.

Table 1. Some commercially important barley varieties classified according to their reaction to DDT

Resistant	*Susceptible*
Archer	Domen
Carlsberg II†	Freja†
Earl†	Hen Gymro
Kenia	Herta†
Maythorpe†	Ingrid
Pioneer†	Isaria
Plumage Archer†	Minerva
Proctor†	Rika†
Provost†	Spratt
Spratt Archer†	Vada

†Recommended varieties on N.I.A.B. List, 1959.

The first indication that this reaction is genetically controlled was obtained from the parentage of some of the above varieties. For instance, Proctor (resistant) was derived from a cross between two resistant varieties, namely, Kenia and Plumage Archer, whilst Rika, developed from a cross of the resistant Kenia and the susceptible Isaria proved to be susceptible. The full genetic mechanism of this gene was obtained by studying the F_1, F_2 and F_3 generations from crosses of resistant $\times$ susceptible parent plants, and backcross tests. The progenies of resistant $\times$ resistant crosses were all resistant

to spray damage; those of susceptible × susceptible were all susceptible, while inheritance studies on resistant × susceptible crosses gave the following segregation (Table 2).

Table 2. Reaction of progeny from crosses of resistant × susceptible plants

	Number of plants and progenies						
	Observed			*Expected*			*Prob-*
Generation	*Resist.*	*R/S*	*Susc.*	*Resist.*	*R/S*	*Susc.*	*ability*
F_1	–	–	72	–	–	72	
F_1 backcrossed to R	8	–	10	9	–	9	0.9 – 0.5
F_2 plants	83	–	203	72	–	214	0.5 – 0.1
F_2 plant progenies†	82	135	66	71	141	71	0.5 – 0.1
F_3 plants from 135 segregating F_2 progenies	327	–	889	304	–	912	0.5 – 0.1

†Three F_2 plants failed to produce seed.

It is clear from this evidence that the varietal response to DDT is controlled by a single major gene with susceptibility dominant to resistance. Crosses involving 6 genetic stocks have now been made in an attempt to identify the linkage group to which this gene is attached, and its relation to other genetic markers.

Various experiments have shown that it is the DDT fraction in the proprietary sprays which is responsible for the reaction, and not the solvents and emulsifiers. When the plants were sprayed there was no effect except at very high concentrations when localised lesions appeared which could not be confused with the chlorotic effect over the whole leaf brought about by the DDT fraction. All the proprietary compounds containing DDT in the various formulations and concentrations, approved by the Ministry of Agriculture during 1958, were tested and each gave a positive reaction. One of the formulations tested involved applying DDT as a vapour, to which barley also gave a typical reaction thus indicating that the nature of the leaf surface was not the critical factor in determining resistance or susceptibility. Several other chlorinated insecticides and organo-phosphorous compounds have been tested, to none of which has barley shown a similar reaction. The normal strength of application used for these investigations was 1 part DDT to 500 parts water, but typical reactions were obtained from varying the concentrations, ranging from 1 DDT : 50 water, up to 1 DDT : 2,000 water. Barley plants react at all stages of growth and over a wide range of temperature conditions, but at the higher temperatures growth is more rapid and the response of susceptible plants is far more striking.

A noteworthy feature of this clear-cut differential reaction to DDT lies in its potential value as a means of determining quickly and accurately in the early seedling stage the degree of contamination in any varietal stock. Suitable procedures have already been outlined (Griffiths and Hayes, 1959) whereby varietal purity can be rapidly assessed in the field nursery or glasshouse. The tests have shown that many varieties of barley in commerce do contain an admixture which is not readily detectable in the growing crop.

In order to assess the effect of DDT spray on the productivity of the crop, a field experiment was laid down during 1959, which involved two high-yielding, stiff-strawed varieties, Proctor resistant, and Rika susceptible, to damage by DDT. Both varieties were sprayed together in a split-plot field trial. There were 8 treatments, in a combination of control, 1, 2 and 3 sprayings, at intervals of 1, 2 and 3 months after germination.

Table 3. Yield of a resistant and susceptible variety of barley after spraying with DDT in the field (relative to Rika (unsprayed) = 100)

	Sheaf weight		*Grain weight*	
Treatment	*Rika(S)*	*Proctor(R)*	*Rika(S)*	*Proctor(R)*
No spraying (control)	100	94	100	93
Mean of 1 spraying	72	96	64	97
,, ,, 2 sprayings	59	94	47	97
,, ,, 3 ,,	37	94	28	95
S.E.	±4·9	±5·7	±4·5	±5·3

Proctor, the resistant variety, suffered no damage by spraying even three times during the season ; Rika, however, the susceptible variety, showed a progressive reduction in yield of grain and straw after each spraying treatment. Three sprayings proved highly detrimental to the productivity of the crop giving only 30% of the grain yield of the unsprayed plots.

The yield of grain from plots sprayed at anthesis proved to be 59% of that from unsprayed plots and may be due entirely to photosynthesis in the ears and stems. It would be of interest to measure the photosynthetic activity of the chlorotic leaves resulting from spraying susceptible barley varieties, as from field observation they do not appear to contribute towards the final yield of grain. In view of this evidence it is possible that the estimates by Watson and Norman (1939), and Porter *et al.* (1950) for the photosynthetic activity of the ears of barley may be conservative in relation to their true contribution to the total yield of grain at maturity.

This sensitivity of certain varieties of barley to DDT spray is of special importance in so far as mixed corn is concerned. In districts where it may be necessary to spray with DDT insecticides for the control of frit fly in oats, it is imperative that only resistant barley varieties be included in the mixed crop.

The gene which controls reaction to DDT has several interesting physiological features, the growth of leaves is arrested immediately, but 7 to 9 days elapse before signs of chlorosis appear. There are no grounds for believing that DDT is translocated within the plant, since the action appears to be confined only to leaves which have been sprayed. Further the *Cucurbitaceae* are notoriously susceptible to damage by sprays containing DDT, and damage has been reported in such widely diverse crops as carrots and coffee.

Davidson (1958) has shown that certain individuals in populations of *Anopheline* mosquitoes show resistance to DDT and that this resistance is also due to a single recessive gene. Biochemical work by Sternberg *et al.* (1950) has also shown that part of the DDT resistance in flies depends on an enzyme which converts the DDT into the harmless compound DDE. This enzyme appears to be present in all resistant strains, and absent, or nearly so, in susceptible ones. It is a matter for speculation as to whether the same enzyme complex is in operation in these two widely separated organisms in the Plant and Animal Kingdoms respectively. It is possible that a study of the nature of the enzymes responsible for the inactivity of the DDT on plants may be of value in elucidating some of the problems which confront the entomologists dealing with resistant strains of insects. It has been suggested by Winteringham and Barnes (1955) that the preparation of an active and specific dehydrohalogenase would be an interesting and possibly useful research tool.

It may be noted that the old 'land' varieties of barley show different reactions. Spratt and Hen Gymro, for instance, are susceptible while Archer and Gull (the 'land' variety from Sweden) are resistant. Thus this gene does not appear to have had any advantage or disadvantage associated with it during the evolution of the cultivated barleys.

The use of insecticides on agricultural crops is recent, and the reaction to DDT, which as far as can be ascertained is not expressed in any other way, has therefore had no selective influence on plant breeding programmes. Reference to Table 1 emphasises that the alleles of this gene are randomly distributed through the varieties of barley in commerce. It will be a simple matter from a plant

breeding point of view to develop new varieties of barley which are resistant because of the fairly large number of well-adapted resistant types already available.

The stimulating feature of this work is that striking physiological differences of this nature, which require environmental factors for expression, are evident in apparently uniform material, and this latent variability within cultivated crops might be larger than anticipated. Plant breeders of the future may still be able to make big advances in the light of new techniques of culture even though the basic material now appears to be relatively uniform.

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RELATIONSHIP BETWEEN VEGETATIVE AND SEXUAL COMPATIBILITY IN *TRIFOLIUM*

ALICE M. EVANS

During investigations into species relationships in the genus *Trifolium*, individual genotypes of the different species were grafted together prior to crossing, to determine whether this would help to break down the very strong barriers to hybridisation which exist in the genus. At the same time, it was considered that if grafting could affect the interspecific compatibility, then it could feasibly have an effect on the self-incompatibility of the individual genotypes. Hence a parallel investigation was set up to elucidate the effect of intraspecific grafting on self-fertility.

It was considered that taxonomically-related species would be more likely to be related genetically, so species (of the tribes *Euamoria* and *Eulagopus*) taxonomically related to white clover (*T. repens*) and to red clover (*T. pratense*) respectively, were used. For the purpose of this paper, the data are confined to one interspecific cross, namely *T. hybridum* and *T. ambiguum*, and, for the intraspecific grafting and selfing, reference will be made to *T. pratense* only. The results, however, are largely true for all *Trifolium* spp. investigated.

Wedge-grafting of seedlings was the method adopted and ungrafted controls were retained of all plants used. It was important to distinguish between grafts which were unsuccessful due to faulty technique, and those which were unsuccessful because of the 'incompatibility' of the components. The error was reduced by replication, repetition and standardisation of the conditions under which the grafts were made. Graft compatibility was classified into compatible scions which flowered normally, incompatible scions which died, and an intermediate group of pseudo-compatible scions which grew abnormally and did not flower.

Effect of grafting on interspecific compatibility

Table 1 shows the graft compatibility of *T. hybridum* and *T. ambiguum* at two levels of ploidy; diploid ($2n = 16$) and colchicine-induced tetraploid ($2n = 32$) *T. hybridum*, and diploid ($2n = 16$) and naturally-occurring hexaploid ($2n = 48$) *T. ambiguum*. The number of plants grafted and the percentage of genotypes occurring in the three compatibility groups are recorded.

Table 1. Graft compatibility of T. hybridum *and* T. ambiguum *at two levels of ploidy*

Stock	Scion	No. of plants	Percentage genotypes		
			Com-patible	Pseudo-com-patible	Incom-patible
T. ambiguum (2x)	*T. hybridum* (2x)	72	25	16	59
T. hybridum (2x)	*T. ambiguum* (2x)	72	17	25	58
T. ambiguum (6x)	*T. hybridum* (4x)	54	40	27	33
T. hybridum (4x)	*T. ambiguum* (6x)	54	23	30	47

Three major points emerge from the results. Firstly, it is evident that when *T. ambiguum* is the stock there is an appreciably higher percentage of compatible grafts than when *T. hybridum* is the stock ; secondly, polyploids show greater compatibility, and thirdly, there is a profound effect of genotype within any particular species combination which accounts for the division into the three compatibility groups.

The results of the graft compatibility classification were used to make a parallel series of interspecific crosses between *T. ambiguum* and *T. hybridum*. The sister clones of the grafted plants were retained as ungrafted controls and three types of interspecific crosses were made :

(*a*) Graft-compatible *T. ambiguum* × graft-compatible *T. hybridum*

(*b*) Pseudo-graft-compatible *T. ambiguum* × pseudo-graft-compatible *T. hybridum*

(*c*) Graft-incompatible *T. ambiguum* × graft-incompatible *T. hybridum*

These results were compared with stock × scion and scion × stock interspecific crosses of successful grafts of the plants in group (a). Both scion × stock and stock × scion crosses were made, but the reciprocal differences were small so the results were pooled. Prior to pollination, the florets were emasculated by removing the floral parts with a forceps, leaving only the pistils enclosed by the calyx (Williams, 1954). The number of embryos 10 days after pollination was recorded in all the hybridisations and are shown in Table 2.

Table 2. Hybridisation of genotypes compatible as grafts, and of the ungrafted controls

First named species as ♀ parent	*No. of graft-com-patible plants*	*Percent embryos obtained*			
		Graft com-patible plants	*Ungrafted plants*		
			Cross (a)	*Cross (b)*	*Cross (c)*
T. ambiguum (2x) × *T. hybridum* (2x)	18	21	18	3	1
Reciprocal cross	12	16	12	4	0
T. ambiguum (6x) × *T. hybridum* (4x)	22	15	11	0	0
Reciprocal cross	12	9	7	2	0

The outstanding feature of the data is the difference in fertility of the three graft compatibility groups. Graft-incompatible plants (c) were also virtually sexually incompatible, while the pseudo-graft-compatible plants (b) showed a very low fertility. Plants classed as graft-compatible (a), on the other hand, showed a measurable level of fertility. It is also to be noted that crosses made with grafted plants gave a similar but slightly higher number of embryos in each case.

Other points of interest which emerge from the results include the difference between the compatibilities of the reciprocal crosses. In both cases where *T. ambiguum* is the female parent, there is a higher percentage of embryos produced than when *T. hybridum* is the female parent. The species do not show greater sexual compatibility at the higher ploidy level, but this is possibly due to the fact that the incipient embryos would be pentaploid and there might be failure of embryo development due to unbalance of the tissues of different ploidy.

The work shows that there is a relationship between sexual and vegetative compatibility, namely, that sexually compatible genotypes are generally vegetatively compatible, and conversely, genotypes that are vegetatively incompatible are generally sexually incompatible. The results confirm those of Addison and Tavares (1952) who speculated that the success of hybridisation on the one hand, and the outcome of grafting on the other, have a common physiological basis. Harland (1955) made a statement supporting this view that " if two species can be grafted it seems that they possess in common some factors of a biochemical nature — they are biochemically related." The foregoing results do not clearly confirm those of Michurinist geneticists who have shown that *vegetative rapprochement* is a means of breaking down species barriers, thus making crosses compatible. However, it becomes apparent from this work that vegetative compatibility of the genotypes can be used as a sieve to select those parents most likely to be sexually compatible.

Effect of grafting on intraspecific compatibility

The only obvious physiological change noted in the inter-specific grafted plants was the increased self-fertility of the scions. In order to determine whether this feature was operative, vegetative and sexual compatibilities were studied intraspecifically using plants of *T. pratense.*

In Table 3 the results of grafting between and within plants of *T. pratense* are shown.

Table 3. Graft compatibility in T. pratense

	No. of plants	*Percentage grafts*		
		Flowered normally	*Died before flowering*	*No graft union*
Intra-plant grafting (homografts)	30	30	20	50
Inter-plant grafting (heterografts)	30	50	10	40

It will be noted that 50% of the self-grafts failed and a further 20% were stunted and failed to flower. With inter-plant grafting, on the other hand, only 40% failed and 10% died before flowering. Normal growth of scions and abundant flowering was obtained in 50% of the heterografts as against 30% of the homografts.

Table 4. Self-compatibility of stocks, grafts and ungrafted controls of T. pratense

Selfing of T. pratense	*Mean percentage seed set*
Ungrafted controls	0.8
Stocks	1.0
Homografts	4.8
Heterografts	9.2

On selfing the stocks and the ungrafted control plants, the mean percentage self-fertility was 0.8 and 1.0, but on selfing the scions 62% of the plants gave seed, the mean percentage seed set of homografts being 4.8 and heterografts 9.2 (Table 4).

Self-sterility in *T. pratense* is governed by a multiallelic system of 'S' genes similar to the *Nicotiana* hypothesis (East and Mangelsdorf, 1925). The two alleles present in the pollen of diploid red clover

are equally effective but when the same alleles appear in the style, pollen-tube growth is inhibited, and no fertilisation takes place. In this multiallelic system there is independent assortment of the alleles. A possible explanation of the results that homografts were less successful than heterografts (Table 3) is that the 'S' gene system might be operative in the vegetative tissues thus reducing the percentage success of self-grafts but not completely preventing graft compatibility. On selfing homografts the percentage seed set is greater than the controls but not as great as the heterografts. Williams and Silow (1933) have shown the existence of 'pseudo-fertility' in the self-sterile *Trifolium* spp. which would account for the 0.8% self-fertility of the control plants. This is accentuated after homo- and hetero-grafting and it is possible that the two alleles do not now function as previously. One allele is much weakened in its effect and the inhibition to pollen-tube growth in the style is also weakened. Denward (1956) in a similar experiment goes one step further and suggests that the genotype of the female parent determines the function of the pollen, and that this approaches a sporophytic type of incompatibility. He called the group of plants where increased self-compatibility after grafting occurred "the labile group." The present work has so far only provided an indication that the 'S' gene system has been partly broken down by grafting.

If we now take the wider view, it would appear that the breaking down of self-incompatibility is important too in species crossing. Lewis (1955) has shown that there is a relationship between self-compatibility and interspecific compatibility and he has represented this as follows :

Style		*Pollen*	
S.I.	×	S.C.	= Incompatible cross
S.C.	×	S.I.	= Compatible cross

Where the female parent shows natural or induced self-compatibility the cross is more likely to be compatible. Examples are found in the genus *Lycopersicum* (Lewis, 1955) and in *Petunia* (Mather, 1943). Interspecific hybridisation in *Trifolium* has been largely carried out in the past with self-incompatible species. Possibly more success could be achieved in producing hybrids in the genus if the self-fertile species were used as female parents, or if self-compatibility were induced in the female parent prior to crossing.

The nature of the interspecies incompatibility system in *Trifolium* may well be genetically similar to the self-incompatibility system and the breakdown of the latter may aid in the breaking down of the former.

We have seen that there is a parallel between sexual and vegetative compatibilities. Possible explanations for the relationship can now be considered and many workers have already demonstrated that the pollen tube/style and scion/stock compatibilities are physiologically determined and are a function of the specific proteins of the component plants.

Straub (1948) investigated the affinity between the stylar tissue and the growing pollen tubes of *Petunia* clones and he concluded that affinity was related to protein specificity of the tissues. Similarly Linskens (1955), working on the same material, extracted carbohydrates and proteins from the stylar tissues by electrophoretic separation, and he again came to the conclusion that the carbohydrate/protein complexes were the products of a specific mutual reaction between the style and the pollen tube. Working on *Oenothera organensis* Lewis (1952) compared the serological reaction of the pollen tube/style with the antigen/antibody reaction in animals.

Graft compatibility has also been explained in terms of serology. Kostoff (1929) affirmed on the basis of innumerable experiments that plants could be induced to produce antibodies against foreign proteins, and he showed that this phenomenon of the production of antibodies is realised in grafting. He concluded that the scion developed antibodies against the proteins of the stock plant, and that the degree of precipitation gave an idea of the affinity between the plants. Silberschmidt (1935) undertook to verify the findings of Kostoff (1929) and he came to the conclusion that the precipitates obtained were not a consequence of the quantity of antibodies in the scion but might be due to the accumulation of proteins. Protein specificity is one of the important foundations of the differences between species, and studies of this specificity will undoubtedly shed more light on the relationship between species. These considerations may yield a profitable line for future work, but up to the present the practical significance to the plant breeder and geneticist of this relationship in *Trifolium* is that graft compatibility can be used as a screening technique to reduce to more manageable proportions the very large number of parent plants which it is usually necessary to cross before success can be achieved in species hybridisation. Graft compatibility therefore becomes an indication of relationship between species.

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DENSITY OF GRASSES FOR SEED PRODUCTION

Gwilym Evans

Excessive weediness, poor tilth, or wrong dates of sowing have exerted undue influence on seed rate levels for grasses, but generous quantities of seeds have not satisfactorily overcome the difficulties attached to such hazards. Furthermore, dense populations may have resulted in substantial losses of seed yields. This is a problem which has been critically studied at the Station for many years.

Perennial ryegrass

If it were possible to provide species and varieties of grasses which could automatically adjust themselves to plant or tiller densities, the task of successful seed production would be simplified. This feature exists to a limited extent among farm crops ; for example, some new varieties of oats bred at this Station, and our experiments with leafy varieties of perennial ryegrass, have given encouraging results in this direction. Pasture varieties of perennial ryegrass broadcast for seed at various densities with or without a cereal cover crop have been shown to be capable of a considerable degree of adjustment. No significant difference in seed yields is found whether the range is from 12 to 36 lb. (Evans, 1937) or from 4 to 20 lb./acre broadcast (Lewis). Similarily the yield is not significantly better in early and late varieties sown at the standard rate of 5 lb./acre in wide drills than at 1 lb./acre (Evans, 1959). Increased tillering appears to compensate for low plant density within these limits and the tiller numbers thus developed become capable of producing full seed crops. Perennial ryegrass is peculiarly flexible in this respect, for the response is similar in such widely diverging types as S.23 pasture variety and Wimmera (Donald, 1954).

Although perennial ryegrass has thus been shown to have high potentiality for self-adjustment the question arises whether there are limits to this process. We have evidence that in fact such limits do exist for this species.

When plants are spaced 12″ apart in wide rows on the one hand, or seed is sown in wide drills at several times the normal rate on the other, the seed yields are significantly reduced. At the lower densities plants are apparently unable fully to exploit the ground, and at the higher the competition is excessive for maximum seed production. Drills sown at the standard rate and ' gapped ' may

a'so show as much reduction in yields as spaced plants, when gaps of 8″ are made in every ft. length of drill. A reduction from normal densities of ryegrass by these methods is much more drastic than a sowing at 1 lb./acre, which made no significant difference to yields (Evans, unpublished).

Other species

When we consider the impact of seed rate on seed yield in other species we find that several are remarkably sensitive to heavy rates (Evans, unpublished). Both meadow fescue and tall fescue react very strongly to heavier-than-normal seed rates, in fact excessively dense stands may lead to *seed crop failure* although vegetative growth may appear satisfactory. On the other hand, by reducing the seed rate for wide drills to one-fifth of the normal a substantial increase is achieved in these species. Drastically further reducing density by growing plants of tall fescue spaced 12″ apart in rows 30″ wide results in still greater positive response in terms of seed yields. This species is much better able to adapt itself to low densities and to exploit ground space than perennial ryegrass. *Phalaris* hybrid S.230 and cocksfoot also react to high and very low densities, but have a greater power of adjustment at the higher densities than have the fescues. Timothy also appears capable of adjusting itself better than the fescues to the higher densities but is nearer to perennial ryegrass in this respect (Evans, unpublished). Although spaced plants have shown an overwhelming superiority over sown seed in most species there still remains the problem of optimum spacing for each variety. We have some evidence to show that nothing is gained by spacing cocksfoot plants at more than 12″ apart in rows 24″ wide (Evans, 1935), and that a spacing of 36″ between drills of sown seed is excessive for meadow fescue, timothy and cocksfoot (Roberts, unpublished).

The problem of sowing at the low rate of 1 lb./acre or less could be solved by using precision drills, or by diluting the seed with a suitable inert material so that ordinary drill machines may be used. Thinning normal densities by mechanical means could undoubtedly improve the yield of some varieties, but it has yet to be shown that this device can produce as good results as are obtained by thin sowing or wide spacing.

Very weedy fields are not commonly used for seed production by professional growers and the evidence is clear that it is more profitable to sow thinly, and if need be afterwards to use a selective weed killer, than to sow thickly in an endeavour to control weeds.

Soil fertility

The above conclusions apply to land of average fertility and for crops not receiving nitrogenous fertilisers. It is known that seminal reproduction is inhibited by an impoverished condition of grass plants, and that nitrogen, on the other hand, is the most potent fertilizer for the induction of seed heads in grasses. Can then fertility in terms of soil nitrogen correct the disability of unsuitable densities? The evidence indicates that nitrogen can correct the depressing effect of excessive sowings in varying degrees, according to species and variety. A pasture type of perennial ryegrass sown broadcast shows a marked capacity for adjustment with the help of nitrogen applied in autumn and spring. When, however, sowings made in wide drills are several times the standard rate for both late and early types of this species, the first harvest year yields are significantly reduced, generous application of nitrogen notwithstanding (Evans, 1959). Furthermore, the fertiliser has not been able to bring the seed yield of ryegrass plants spaced 12″ apart in wide rows to the level of crops for drilled seed (Evans, unpublished).

In tall fescue, meadow fescue, cocksfoot, timothy and *Phalaris* the greater the density the higher is the percentage response to nitrogen, as measured in terms of seed yields for successive harvest years (Evans, unpublished). This response is much greater in some species than in others. For example, nitrogen increases the yield from a very heavy seeding of S.37 cocksfoot by about 50%, whereas from the same treatment S.230 *Phalaris* may show a 500% increase. The reaction of the other species mentioned falls within this range. It is important to observe, however, that although nitrogen increases seed yields of very dense cultures in wide drills such yields are still significantly lower than those from thinner stands, more especially in the first harvest year.

The damage from overcrowding may still remain in the presence of ample nitrogen. Its pernicious effect persisted in S.37 cocksfoot during the wet summer of 1958 when an application of NPK in the autumn, and of N in the spring, actually reduced the seed yield. In any case generous quantities of nitrogen in relation to average spring and summer rainfall may result in excessive vegetative growth and severe lodging, both of which depress seed yields.

Of particular interest is the question, can nitrogen increase the yield produced from a standard rate of sowing to the levels obtained from 1 lb./acre sowing in wide drills? Perennial ryegrass, whether grown in wide drills or broadcast, shows no reduction in yield at the

standard rate when nitrogen is applied, and similarly *Phalaris*. Nitrogen, however, may fail to overcome the very harmful effect of the *standard* rate on first harvest year seed crops of pasture types of cocksfoot, timothy, meadow fescue and of tall fescue.

Persistency of density effects

The adjustment of densities as measured by seed yields is often significantly incomplete in the first harvest year (Evans, 1959, Evans, unpublished). On the other hand, density effects tend to diminish in subsequent years. A distinct downward gradient persists, however, in some varieties to the third and even the fourth harvest years, with and without applications of nitrogen. Tall fescue and a pasture variety of cocksfoot are typical examples of grasses which fail to adjust themselves to a wide range of seed rates. It seems that competition between the plants fails to reduce the population from heavy sowings to the level of that from thinner sowings and so remains potent in depressing seed yields.

A similar downward gradient persists to the third harvest year in high tillering types of timothy, meadow fescue and *Phalaris* when grown without nitrogen. *With* nitrogen, however, the differences due to rates are progressively reduced : in meadow fescue and timothy they may disappear in the second harvest year seed crop. The behaviour of perennial ryegrass is particularly interesting in the *second* harvest year ; with the addition of nitrogen there is an upward gradient in sympathy with an increasing seed rate, so that a significantly higher yield is produced from a very thick sowing in wide drills than from a sowing of 1 lb./acre. This result is the opposite of that obtained in the first harvest year. Furthermore, the same tendency is observed in early, as in late, heading types and shows adjustment *in excelsis*.

In addition to the factor of fierce inter-plant competition for the essential requirements of plant life, leading to an increased percentage of casualties as the sowing densities increase, another important factor appears to have a bearing on this situation, that is, the relative longevity of plants under seed production conditions. Even where inter-plant competition is inoperative, as in widely spaced plants of ryegrass, a considerable proportion of the plants may die after the first harvest seed crop. In this respect, ryegrass is peculiarly propense and contrasts strongly with such grasses as tall fescue and cocksfoot, and partly explains the difference in the persistence of density effects.

Varietal interaction

The capacity of a variety for tillering may greatly influence optimum plant density for maximum seed yields. It may be found that the optimum numbers in high tillering types may be much fewer than in the low. In one experiment the density effects of the high tillering cocksfoot S.143, with and without nitrogen, persisted into the *fourth* harvest, but in another experiment, where the fertiliser had been applied, they had disappeared in S.37 cocksfoot (lower tillering) before the third harvest.

As the number of seeds per pound varies enormously *between* and *within* varieties this factor should be carefully considered for each *stock*. A very ' light ' sample of S.143 may have 780,000 seeds per lb. whereas a very ' heavy ' sample of S.37 may contain only 320,000, and although density may not affect numbers per lb. of seed produced (Evans, 1937 ; Evans, unpublished), other environmental factors may cause this relationship to be reversed. Thus proper attention to the constitution of a pound of seed would contribute towards efficiency in seed production.

Conclusion

We now have evidence that the customary rates of sowing grasses cause large losses in seed yields. Thus a new step forward is taken when we realise that much lower plant densities than normal are required for maximum seed yields.

It is clear that to express fully the seed yield potential it is necessary to determine the most suitable density for each variety or growth form within a species. Furthermore, the density of plant population of each variety must be considered in relation to fertility level.

By thinking in terms of establishing the optimum number of plants per unit area for each variety, we can look with confidence to obtaining substantially higher yields of seed per acre. In addition, wastage of valuable seed stocks is avoided and easier harvesting is promoted.

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STUDIES ON THE NITRATE NITROGEN CONTENT OF HERBAGE

G. ap Griffith

When grass first came into its own some standard for assessing its value became essential. For many years the so-called crude protein content remained the only criterion (apart from dry matter yield), partly because of the relative ease with which crude protein could be determined, but also partly because there was a conviction that protein was the most valuable constituent of the herbage. The present tendency, however, is to depreciate somewhat the value of protein and to emphasise the energy-producing value — the digestible energy of the grass.

In so far as this represents a swing only against the conception of crude protein it is both logical and desirable, but any tendency to forget the essential value of the constituent protein must be avoided. More information is needed about the nature of the complex which goes under the name of crude protein. This is a conventional figure arrived at by multiplying the nitrogen percentage by 6.25 and embodying two assumptions, namely (i) that the whole of the nitrogen is in the form of protein and (ii) that protein has a nitrogen content of 16%. The second assumption approximates to the truth which the former does not. Accurate information is now wanted for each herbage species at different growth stages and under different systems of management as to what is the true protein content and of what proteins it is made up, what is the nature of the non-protein nitrogen, and what feeding value, if any, it may have. Until such information is available the mere mechanical out-turn of crude protein percentages is of doubtful value.

A start has been made here to examine in more detail the non-protein nitrogen, and a chance observation almost at once led to a simplification of the initial objective. It was found that a composite sample of herbage material, made up of many hundreds of samples which had passed through the laboratory in the course of routine analysis, had an unexpectedly high content of nitrogen in the nitrate form. This implied that some of the herbages which had made up the sample must have had very high nitrate contents. A search was at once made for likely material, with immediate results.

An experiment had been conducted by the agronomists at the Station to study the growth of eight grasses as swards and as spaced plants, with and without nitrogen, at two widely different altitudes. Very high nitrates were found in the spaced plants ; the swards

normally showed less, but in the swards too in June and September the nitrates were high. The nitrate nitrogen represents an excess of uptake over utilisation and the difference between spaced plants and swards was due to the fact that they had both received the same amount of nitrate per unit area of land and therefore the excess of nitrogen per plant was greater for the spaced plants.

The results followed a similar pattern at both high and low altitudes, except that at the higher altitude the effect of the lateness of the growing season was shown in a higher nitrate content in the swards at an earlier date.

The principal point of interest in these first observations was the marked differences in the species and varieties. In the spaced plants at both altitudes in primary and recovery cuts S.23 ryegrass and S.143 cocksfoot showed a consistently higher nitrate content than the other grasses. As swards, however, S.24 was consistently higher than S.23. Other differences were also noted for which no explanation can yet be offered, but the fact that they do exist will be of interest to the grass breeder if the question of breeding for better utilisation of applied nitrogen becomes important.

In these experiments the amount of nitrogen applied was high, totalling over the growing season some 12 cwt./acre nitrochalk. Accumulation of nitrate in such circumstances was not unexpected, especially as the results indicated a tendency to accumulation at periods of arrested growth which, when taken in conjunction with high nitrogen manuring, might be expected to result in nitrate accumulation.

It was decided to take the investigation further and this time, through the courtesy of Dr. Rice Williams, material was examined from an experiment conducted earlier by the National Agricultural Advisory Service (Wales), at Trawscoed (ap Griffith, 1960). The special interest in this material was that it came from a different district. The nitrogen had been applied as sulphate of ammonia, which might reasonably be expected not to exaggerate any tendency to nitrate accumulation, and there were several levels of application, 0, 2, 4, 6, 8 and 12 cwt./acre. Three different grass mixtures were compared, and perhaps most important of all, the nitrogen had been applied in late April, a time corresponding to local farming practice, whilst the herbage was not cut until six weeks later, which again might be expected not to exaggerate any nitrate effect.

The results showed a linear rise of nitrate nitrogen with increasing nitrogen application, through about 400 p.p.m. nitrate nitrogen on dry matter basis at the 4 cwt. level, to 2,000 and more

p.p.m. at the 12 cwt. level (Fig. 1). A similar close linear relationship existed between the nitrate content and the crude protein content (Fig. 2). Up to a crude protein content of 18–19% there was little, if any, nitrate present, but after this point nitrate rose linearly with crude protein through about 500 p.p.m. at about 22% to 2,000 p.p.m. at 29%.

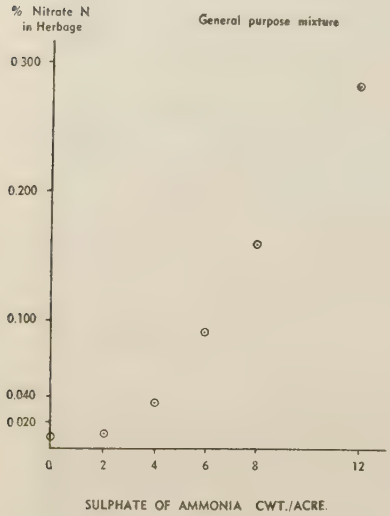

Fig. 1. Relation between nitrate N of herbage and fertiliser level.

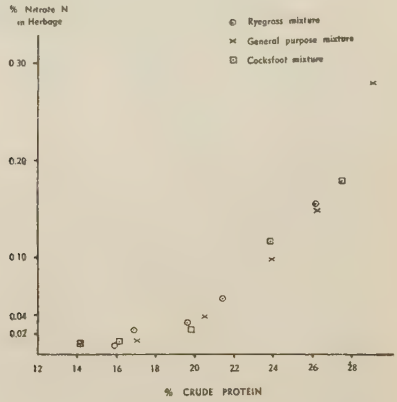

Fig. 2. Relation between nitrate N of herbage and crude protein.

A general relation between crude protein and nitrate nitrogen is of course to be expected, but it should be understood that such a relation exists only for material which has been treated alike as to date of application of N and date of sampling. Variation in these dates (as in the earlier experiment) can lead to high nitrate with low crude protein or vice versa.

These results show that nitrate accumulation is an abnormality which does not of necessity appear only with excessive nitrogen applied unseasonably with too short an interval after manuring to allow the plants to dispose of it. They show also that the use of nitrogen in the ammoniacal form does not prevent the accumulation.

The search was continued for other cases of high nitrate content. The *Brassicae* seemed likely material, and samples of rape supplied by my colleague Mr. T. D. Johnston showed some of the highest

contents yet found. Following on this Mr. Johnston laid down an experiment to provide further information (ap Griffith and Johnston). Nitrochalk was compared with sulphate of ammonia at two moderate levels of nitrogen (30 and 60 lb./acre nitrogen) in three applications on 15 August, 29 August and 12 September respectively, and at two cutting dates, 7 October and 12 November. The N applied on 15 August gave no nitrate accumulation at either date of cutting, or either level of nitrogen; N applied on 12 September showed nitrate accumulation at both levels on 7 October which had disappeared by 12 November. The N applied on 12 September showed nitrate accumulation at both levels on 7 October which persisted to 12 November. There was no difference between nitrochalk and sulphate of ammonia in respect of nitrate accumulation.

Concluding these preliminary observations an examination was made of oat herbage supplied by Mr. J. D. Hayes. He had grown winter oats to find whether the crop could be grazed in early spring before being left to produce its grain. Three cwt./acre nitrochalk had been applied on 18 February and this showed up in a considerable percentage (0.17) of nitrate nitrogen one month later, on 15 March.

The importance of these results lies in the fact that mineral nitrate is known to be toxic in its effect on farm animals. In the United States it has been stated that a 500 lb. animal eating 5.5 lb. of hay containing 5% potassium nitrate could be fatally poisoned (Bradley, *et al.* 1940), whilst the lower limit of toxicity has been variously set at 0.5 to 1.5% potassium nitrate. There appears to be little recorded information in this country as to the lethal or sub-lethal effect, but until the contrary is shown it would be prudent to regard with suspicion any material approaching the lower levels referred to. In terms of nitrate nitrogen these would be 0.07 to 0.2%. Quantities of this order have frequently been met with in the present investigation, and it cannot be too strongly emphasised that, with the exception of the first observations, all subsequent work has been on herbage material manured at fairly moderate levels of nitrogen applied at times corresponding with farming practice, and with reasonable intervals between application and sampling. The possibility cannot be ignored that occurrences of nitrate accumulation may from time to time have contributed to digestive and other upsets which in general terms have been blamed on other factors.

A full account of the experiments referred to in this article is being prepared for publication elsewhere.

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DECOMPOSITION OF PLANT RESIDUES IN THE SWARD

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The productive life of individual grass tillers and roots in a grassland sward is of limited duration (Langer, 1956 ; Troughton, 1957). Thus a sward each year produces a large amount of plant debris, which under optimum conditions is rapidly decomposed by micro-organisms providing both space and nutrients for new growth. If, however, decomposition is incomplete, debris accumulates resulting in a ' matted ' sward, which is regularly associated with decline in productivity.

The occurrence of a ' mat ' implies that conditions are unfavourable for the growth of micro-organisms. Of the many factors involved, acidity and low nitrogen are generally considered to contribute to this condition (Davies, 1939). It is also well known that ' mat ' formation is more frequently associated with some grassland species than others, though the reasons for this are not clear. It may well be that residues from certain grasses are not so easily decomposable ; certainly microbial populations on shoot residues of various grasses are both qualitatively and quantitatively different (Griffiths, 1954, 1955).

The need to ensure an adequate rate of decomposition of residues is widely appreciated but the methods adopted to attain this end are essentially empirical. Their soundness cannot be seriously questioned but we may well ask whether in all circumstances they are the most efficient. Improvement may have to await a fuller understanding of the processes involved in the decomposition of plant residues by micro-organisms, about the nature of which very little is known at present. Even less is known about the conditions under which individual species flourish, and practically nothing about any other effects which their activities may have on the growth and development of herbage plants.

At the outset we need to define precisely the microbial populations with which we have to deal. The more usual approach to this problem is to incorporate residues into a nutrient medium and record those organisms which grow and form colonies. This method, however, can be wholly misleading even when the conditions are designed to recover organisms with specific growth requirements.

For example, a soil which for 2 years had been carefully surveyed for fungi was known to contain over twenty species capable of decomposing cellulose. It might be expected therefore that when cellulose was incorporated into this soil some at least of these species would be active in its decomposition. Further experiments, however, showed that the two species actually involved were 'new' and that none of those previously isolated was active. Clearly, the ability of a species to make use of a particular substrate (i.e. plant residue) does not necessarily imply that the substrate will in fact be decomposed in the soil. Consequently it is most important that the description of the microbial population should be based on techniques which facilitate direct observation on organisms which colonise specific residues under defined conditions.

In an attempt to do this attention has been given in the first instance to one major component of plant residues, namely, cellulose. A simple method was developed for studying cellulose-decomposing organisms which was also found to be flexible enough to allow controlled variation of numerous environmental factors. Soil samples, whose pH and nutrient status may be modified, are placed in petri dishes and the moisture content adjusted to any desired level. The cellulose substrate may then be placed in or on the soil and the plates incubated at the required temperature. We have found that lens tissue paper which consists of a very thin layer of interwoven cellulose fibres is particularly satisfactory. When this material is placed on the soil surface continuous direct observation is possible and the colonised material can be readily recovered and stained, permitting even more detailed study.

Using lens tissue the occurrence of cellulolytic fungi has been examined in a number of soils, particular attention being paid to upland soils where decomposition processes proceed slowly. For these soils it is of particular interest to determine the effects of lime and fertiliser treatments on the population of cellulolytic organisms and this has been examined in two ways.

In the first series of experiments lens tissue was cut into small circular discs, 5 mm. in diameter, and these were placed on the surface of soil samples to which various fertilisers had been applied in solution. The number of discs colonised by each species was recorded after incubation for 7 days at 20°C. The results of one experiment designed to examine the effects of phosphate and nitrate in the presence and absence of lime are shown in Fig. 1. Phosphate was applied as potassium dihydrogen phosphate (equivalent to 0.44% P in the soil), nitrate as potassium nitrate (equivalent to

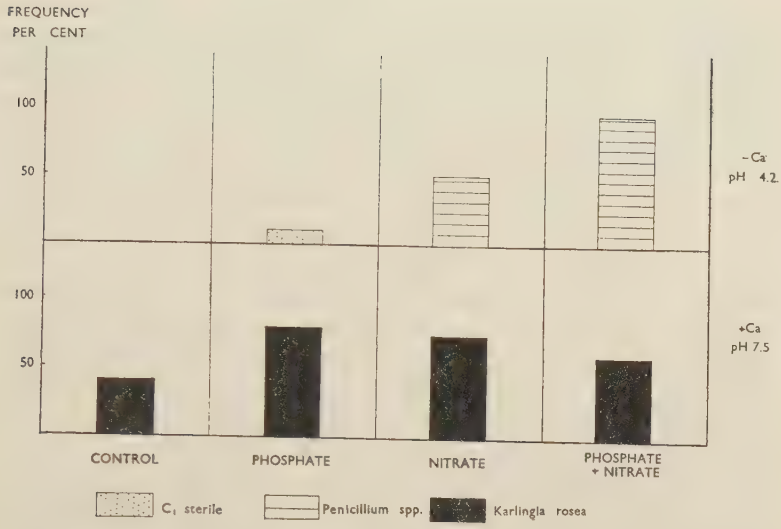

Fig. 1. Effect of lime, phosphate and nitrate on the occurrence of cellulolytic fungi on discs of lens tissue placed on samples of an upland soil.

0.27% N) and lime as calcium carbonate (equivalent to 1.9% Ca). The reaction of the unlimed soils was pH 4.2 and of the limed pH 7.5. In the unlimed series no microbial activity was observed in the control. With phosphate a sterile fungus (C_1) was present, and with nitrate (either alone or in combination with phosphate) *Penicillium* spp. In the limed series there was a remarkable change. In all treatments only one fungus, *Karlingia rosea,* was observed and this was extremely frequent and abundant on soil receiving phosphate alone. While the frequency was also high with nitrate, either alone or in combination with phosphate, the density was markedly less than with phosphate alone. There was, in addition, a marked increase in bacterial activity. Thus although several cellulolytic organisms are present in this particular soil, the activity of individual species is sharply restricted by the mineral nutrient background, an observation which has been confirmed in several other experiments of a similar kind.

It may be considered that the levels at which the fertilisers have been applied are excessive. They certainly provide average values which are higher than would be found in agricultural soils. On the other hand, even higher concentrations must certainly be produced locally when fertilisers are applied in a granular form.

In the second series of experiments fertilisers were applied to simulate the situation when particles of fertiliser are distributed in a discontinuous fashion. The surface of the soil in a petri dish was completely covered with a sheet of lens tissue and a few crystals of fertiliser applied at four separate points. A clear response to treatment was observed after 21 days at 20°C. Around the points of application well defined concentric zones of microbial activity developed whose extent varied with the nature of the fertiliser. Thus nitrate influenced activity over the whole area of a petri plate, whereas the influence of phosphate was restricted to an area approximately 1″ in diameter. The detailed results showed that the species of fungi varied with the distance from the point of application of the fertiliser. Thus with potassium dihydrogen phosphate three main species were recorded: immediately around the point of application *Oidiodendron* spp., then a broad band colonised by *Cladosporium* spp. and at the periphery a zone occupied by *Karlingia rosea*. Beyond this, microbial activity was virtually absent. In addition to the three main species some other organisms occurred sporadically. It is perhaps significant that the sterile fungus C_1, the only important species found when phosphate was applied at a single concentration, was here severely restricted. Evidently small differences in concentration may well have important effects in determining the activity of cellulolytic species.

While the ecology of soil micro-organisms is certainly complex the experimental approach adopted here appears to offer the possibility of providing a clear picture of microbial activity on specific substrates. It is encouraging that already it is possible to detect significant and consistent patterns of behaviour in certain species.

Descriptions of microbial associations, however, are not enough. We need to understand the physiology of the organisms, how they interact with one another and what effect their growth may have on higher plants. There are indications that these will prove fruitful fields of enquiry. Early work by Beijerinck and van Delden (1902) and McBest (1913) has shown, for example, that free living nitrogen-fixing bacteria may be stimulated in the presence of cellulolytic species, and there is also a growing body of evidence that various organic compounds (products of microbial metabolism) exert beneficial effects in increasing the availability of various mineral elements. Organic acids are known to promote the release of phosphate from insoluble and non-available forms (Dalton, *et al.* 1952), and also to prevent or retard the fixation of phosphate in the soil (Mehlich and Drake, 1955). Of equal importance is the role of

organic compounds in chelating and thus increasing the availability of trace minerals such as iron, manganese, zinc and copper (Stewart and Leonard 1956 ; Mehlich and Drake, 1955). Such discoveries have an obvious practical significance, but their exploitation depends upon a clear understanding of the nature and activities of the individual elements of the microbial populations in the soil.

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GROWTH STAGE AND RELATED FACTORS IN GRASSLAND MANAGEMENT

IEUAN DAVIES

The stage of growth at which herbage is grazed or cut is important from two aspects, viz., the nutritive value of the plant to the animal and the influence of grazing or cutting upon the plant and the sward.

Growth stage and nutritive value

The foundation of our knowledge of this aspect was laid in the 1920s (Fagan and Jones, 1924; Woodman, *et al.* 1926), when it was shown that the young leaf of grass is a concentrated protein food. In contrast, the stems are comparatively poor in protein and as they mature they become more fibrous and deteriorate in feeding value much more rapidly than the leaves. This is because the woody parts are not only indigestible but they render more difficult the digestion of the other constituents which they enclose. Herbage cut or closely grazed at weekly intervals is predominantly leafy and high in protein and the few stems that may begin to develop have no opportunity to become fibrous. Extending the interval between grazings to four weeks allows sufficient time for the shoots to become more mature, leading to a better balance of protein and carbohydrate.

As far back as the 1930s it was found that the soluble carbohydrate content is at its highest when the flower heads are just beginning to appear, and declines from June onwards (Norman and Richardson, 1937). Thus while very leafy growth of grass is a high protein concentrate deficient in carbohydrate, when flowering heads begin to appear the balance moves towards a more suitable ratio of protein to carbohydrate and afterwards it may develop very quickly into a feed which is unbalanced for lack of protein and over-abundance of fibre. The high content of soluble carbohydrates at early heading renders this a suitable stage for cutting as silage, not only for its feeding value but also because the sugar component facilitates the process of ensiling.

Growth stage and the well-being of the sward

On occasions the immediate well-being of a pasture may have to be sacrificed for the sake of the animal, but not without compensa-

tion being made at a later period whenever possible. To understand this it is necessary to consider the energy budget of the herbage plant in relation to its growth stage, and finally to examine some factors which influence these relationships.

Energy budget of grass growth. Grasses, like other green plants, are dependent upon their leafage for carbohydrates, or energy foods; green leafage converts light energy into carbohydrate, a large fraction of which is stored in the roots and basal parts of the plant. Removal of leafage by grazing or cutting drastically interrupts these processes, but the remaining leafage continues its work for the benefit of the plant. On the whole, however, the movement of energy materials (sugar-like compounds) is in the reverse direction, i.e., the roots and basal parts are largely drained of their food reserves in order to produce a rapid regrowth of leafy tissue. In an experiment with perennial ryegrass the time needed for new growth to produce sufficient energy material to balance that withdrawn from reserves was about a fortnight, but very much longer in hot dry weather (Sullivan and Sprague, 1943). Under these conditions grazing more frequently than once a fortnight would inevitably lead to reduced herbage production, a gradual wasting away of the plant through lack of food reserves and eventually its death, when it would be replaced by grasses or weeds which are less palatable or less productive. Grazing at fortnightly intervals should enable the pasture to maintain itself at a constant level of production. By lengthening the rest period to one month a greater food reserve is built up and the plant becomes more robust. This picture holds true for the varieties which tend to have an erect habit of growth. With more prostrate varieties such as S.23, the problem of resting the sward is not so acute because, among other reasons, a greater proportion of leaf remains even after close grazing.

Nitrogenous manuring. Nitrogen can exercise the greatest influence upon yield and nutritive value, when other plant foods are adequate. The growth stimulation by nitrogen results initially in an increased demand upon the root reserves, which may lead to a lower content of soluble carbohydrate in the herbage. This can be made good by lengthening the rest intervals proportionately, so as to give the leafage a longer period to compensate for this increased energy expenditure. Here again, the nutritive needs of the animal and the well-being of the sward both call for a longer rest period, certainly not less than four weeks. However, another complication now arises, for the longer the grass leafage becomes the greater will be its deleterious shading effect upon clover. Accordingly, whenever

good clover growth is desired it is wise to restrict the use of nitrogenous fertiliser to the early and late parts of the season.

The transition from the leafy to the heading stage and its implications for silage and hay

The change-over from the vegetative *leaf-tiller* to the reproductive *stem-tiller* for inflorescence development differs significantly from one species of grass to another, and this has an important bearing on the correct management of a sward. Thus in tall fescue the flower head is well developed before the stem-tiller begins to elongate, while in timothy the inflorescence does not differentiate until the stem has grown appreciably. Perennial ryegrass is intermediate in this respect. Associated with these differences it is found that the stem-tillers will remain leafy for a longer period in timothy than in perennial ryegrass and tall fescue. In tall fescue, on the other hand, there is a low proportion of stem- to leaf-tillers; the value is intermediate for perennial ryegrass and high for timothy.

In an early perennial ryegrass like S.24 the developing stem-tillers normally cease to produce leaves during April, and the inflorescences emerge about the second week in May. Management in early spring has a profound influence on the expression of this pattern of development. By not grazing in the spring the most bulky May silage cut is obtained in which the last leaves formed by the stem apices are all retained on the developing stems (Fig. 1a).

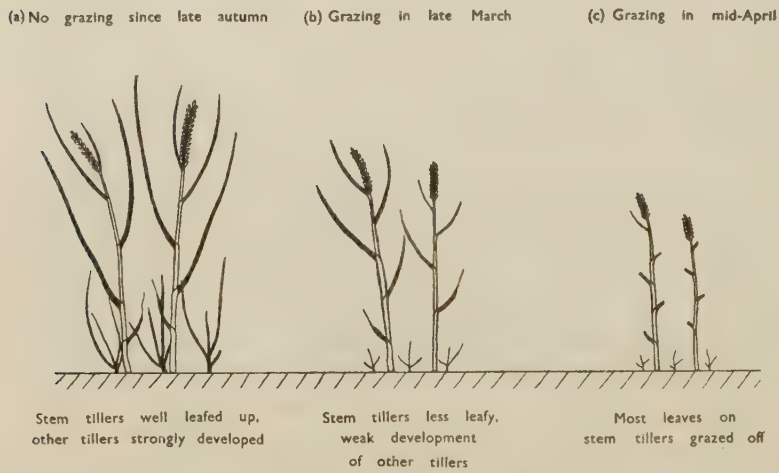

Fig. 1. The tiller composition of a mid-May silage cut following (a) No grazing since late autumn, (b) Grazing in late March, and (c) Grazing in mid-April.

Grazing in late March before the stems begin to form is followed by an immediate regrowth of leaf-tillers. These will develop into relatively leafy stem-tillers by mid-May, which are nutritionally balanced and admirably suitable for silage (Fig. 1b). The leaf-tillers at this stage, although numerically important, contribute little to the yield of herbage.

Grazing until mid-April leads to a different result. The tillers which will contribute the bulk of the ensuing silage cut have ceased producing leaves by this time, and in the most mature the last leaves will have been grazed off before stem formation begins. Hence by mid-May there will be quite a proportion of stem-tillers with virtually no leafage, others with one or two leaves, and only the least mature and smallest of the stem-tillers with three or four leaves (Fig. 1c).

In an extreme instance where sheep had been allowed to graze until late April, after which a liberal dressing of a compound fertiliser was applied, the growth of ryegrass by the second week of May although short was particularly stemmy. This clearly points to the desirability of putting up ryegrass for silage at least 5 or 6 weeks before it can be expected that heads should begin to appear, i.e., late March for early-flowering varieties, and about 3 weeks later for pasture types.

Generally a mid-May cut of an early perennial ryegrass removes the stem apices of most of the potential stem-tillers. The consequent death of these tillers results in the channelling of the nutrient reserves into the rapid recovery of the less mature tillers present at the time of cutting, as well as into the development of a new crop of tillers from buds upon the stubble of the stem-tillers removed in the silage. Thereafter only a small proportion of the tillers develops flowering stems. However, when there had been hard grazing in February the regrowth after a May silage cut was found to develop rapidly into a very stemmy condition. This is because the early grazing had delayed stem formation until after the May silage cut in a large proportion of the tillers.

Perennial ryegrass is pre-eminently a grazing plant; the taking of a hay crop or a late silage cut, i.e., later than the head emergence stage, tends to weaken the sward. On the contrary in timothy the taking of hay has no deleterious effect and for the extreme hay types this management is necessary for the continued well-being of the sward. The differences between the two species in their behaviour are related in large measure to the differences in morphology already indicated.

In timothy when lenient spring grazing is continued until stem formation begins and this is followed by a silage cut about five weeks later, the stem-tillers comprising such a cut are relatively leafy. Each tiller bears 2–4 leaves and there are no leafless stems such as those occurring in perennial ryegrass treated in this manner. This is due to the later cessation of leaf production relative to stem elongation in timothy.

The amount of spring grazing available varies markedly between varieties. S.51 timothy provides grazing about 3 weeks earlier than the commercial types, and it can be grazed later into the spring without prejudicing a later silage cut. This is related to the time when stem formation begins. S.51, although it makes earlier vegetative growth in spring, does not develop stems until about mid-May, 10–14 days later than in the commerical varieties. Of greater significance is the fact that early spring defoliation of the commercial varieties markedly reduces their production and persistency, whereas S.48 and S.51 do not react in this way.

Since in timothy a very large proportion of tillers develop stems, the difference in the time of their formation has a clear-cut effect on production following cuts or grazings at critical stages. Thus, cutting American timothy in mid-May involves the removal of the vast majority of active stem apices. Accordingly, the recovery growth, from a newly-developing crop of tillers, is extemely slow, and for ten days or so nothing but stubble is in evidence.

A silage cut of S.51 in early June, or of S.48 a few days later, or a hay cut of either variety, generally leads to a similar result. Such a slow recovery contrasts sharply with perennial ryegrass and meadow fescue, and even more so with cocksfoot. In these species the leafy tillers, which are invariably present, ensure a rapid recovery.

In S.51 and S.48 the hay stage is attained in late June or early July, i.e., 3 or 4 weeks later than meadow fescue. The use of timothy in conjunction with meadow fescue, therefore, tends to ensure leafiness when silage or early hay is made at the correct stage. The fact that in meadow fescue the taking of a silage or hay cut is not followed by a 'dead' period, as in timothy, is an additional complementary characteristic of this species. However, for the fullest exploitation of the early spring potentialities of S.51 timothy, it should be sown with white clover only.

Conclusions

In practical sward management the criterion upon which the time of cutting or grazing is based is the combination of a relatively

leafy growth with a yield which warrants harvesting, or which allows of rapid consumption by the grazing animal. Management strictly according to growth stage is in many instances not practicable, owing to the wide fluctuation in yield at a given growth stage from season to season. Nevertheless attention to the growth stage at which cuts or grazings are taken, especially during April-May, is necessary for the full utilisation of herbage growth and for the continued well-being of the sward.

With good management the farmer is able to cater for the needs of his animals and at the same time to attend to the maintenance of the sward. Thus rotational grazing, especially for dairy cattle, is preferable to continuous or haphazard grazing, because it provides a more balanced feed for stock and simultaneously allows the sward to build up food reserves, which ensures a continued high level of production. Similarly, for a perennial ryegrass sward the taking of a silage cut in mid-May results in a crop of ideal quality and prevents the loss of food reserves, as happens when cutting is delayed. It is where animal requirements and the dictates of 'good' sward management appear to conflict that the greatest care is needed, and efforts must be made so to plan the grazing programme as to avoid such conflicts.

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CONDITIONS INFLUENCING PRIMARY GROWTH AND REGROWTH OF PERENNIAL RYEGRASS

ALISON G. DAVIES

The pasture physiologist aims to determine the factors which are important in the efficient production of grass in a sward. The situation, however, is usually complex and dynamic, involving not only a mixture of varieties and plants at different stages of growth, but also a changing pattern of growth set against the background of a changing environment.

Useful information can only be obtained, therefore, by robbing the problem of its complexity and attempting to consider the effect on production of a limited number of factors, such as inter-plant spacing and level of applied nitrogen. In this way it should be possible to appreciate the agronomic characteristics of a grass variety, and even to guide the breeder on the most desirable features to incorporate in a new variety.

This method of approach has been employed in a study of the growth and regrowth after cutting of S.24 ryegrass when planted at different spacings (2, 4, 6 and 12″), and after the application of different levels of nitrogen (0, 4 and 12 cwt./acre/nitrochalk per annum). The fertiliser was mixed with soil and applied at three-weekly intervals during the growing season.

Information was obtained in the form of production curves, initial cuts being taken in 1958 from four sets of plots to provide the *primary curve* showing the increase in growth above cutting level from early spring to the hay stage. After the primary cuts the course of regrowth was studied by splitting the plots into three subdivisions and cutting each in turn. This provided data for the *regrowth curves.*

Tillers and heads (if present) were counted before most of the cuts. The results presented and discussed in this paper were, for the most part, obtained in 1958. The 1959 data give a similar picture but have been omitted for the sake of brevity. The investigation as a whole will be published fully elsewhere.

The production curves from the 2″ and 12″ spacings are shown in Fig 1 and from them the following observations can be made :

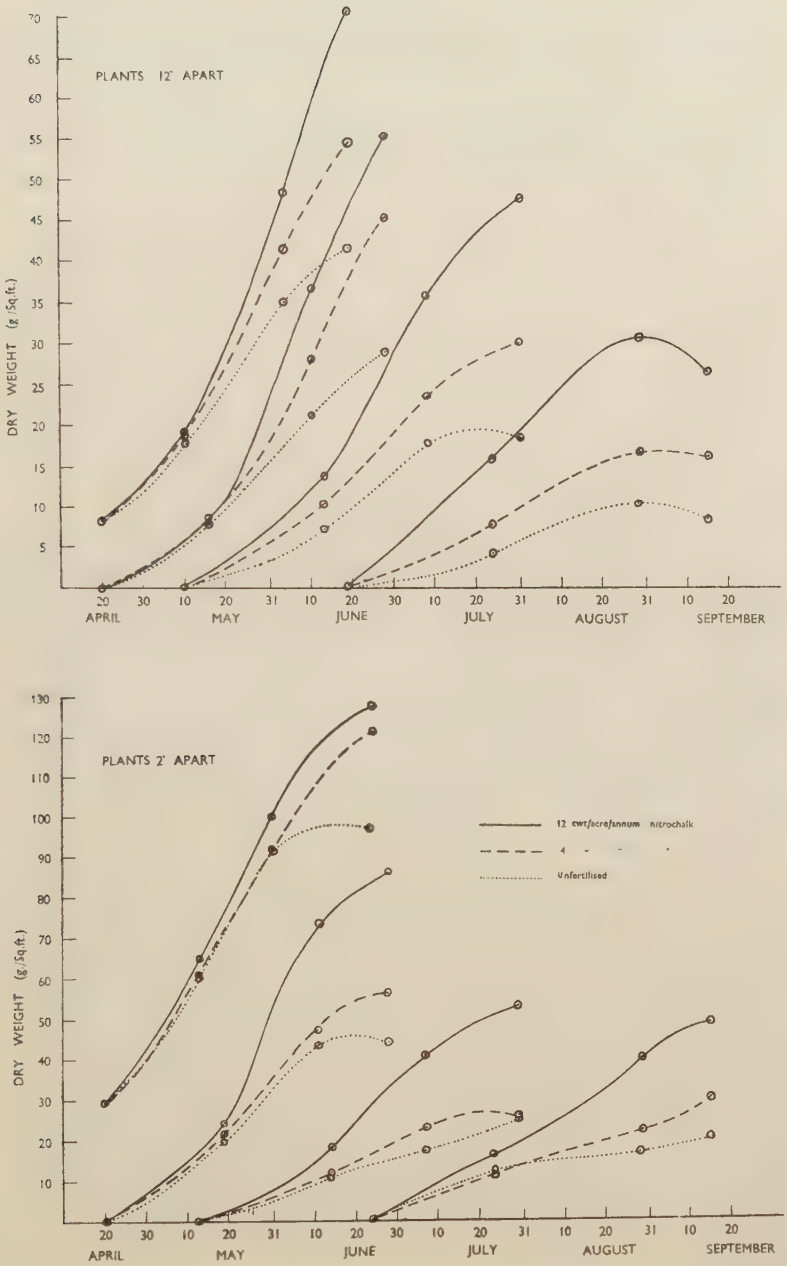

Fig. 1. Primary production curves and regrowth curves 1958. (Regrowth curves, 3rd series, omitted for the sake of clarity).

(1) The general form of the curves tends to be sigmoid.
(2) There is a general seasonal decline in growth rates and in the yields of cuts at the end of each series.
(3) This decline takes place more rapidly at the 2″ spacing.
(4) Yields from the 2″ spacing almost always exceeded those from the 12″ spacing in spite of the greater seasonal decline.
(5) Nitrogen application increased the growth rate.

(1) The sigmoid form of the production curves can be related to the different phases of growth as described by Brougham (1956). In the first phase complete ground cover has not yet been achieved and growth is logarithmic. In the second phase the sward is intercepting all the available light and a steady maximum rate of growth is attained. Ultimately, some kind of ceiling is reached and growth virtually stops. In this instance the reason is almost certainly lack of nitrogen, except at the highest level of fertility when lack of light may be the cause.

(2) The seasonal decline in production is probably associated to a certain extent with seasonal changes in light intensity. In a recent paper Brougham (1959) published similar curves and showed that production over periods of six weeks' regrowth could be correlated with light energy, but such correlations were not obtained for longer periods of regrowth. However, much of the evidence collected in a review by Weinmann (1948) and elsewhere would suggest that when reproductive growth occurs it involves the use of reserves over and above the normal working balance of the plant, so that such a complete correlation in reproductive material could hardly be expected.

(3) The more rapid decline in production at closer spacings seems to be associated with a difference in flowering behaviour. The accompanying table indicates that in all regrowth series but the first the number of heads per sq. ft. was lower at the 2″ spacings. This decline in flowering is particularly well illustrated by the respective ratios of barren to fertile tillers.

Table 1. Average number of heads per sq. ft. and ratio of barren : fertile tillers 1958

	Last cut of	*Last cuts of regrowth series*		
Heads	*primary series*	(1)	(2)	(4)
12″	92	92	64	4½
2″	227½	180	27	Nil
Ratio				
12″	1.76	2.50	4.41	62.22
2″	2.09	3.31	34.37	∞

It seems likely that in the bigger plants a greater proportion of subsidiary tillers becomes competent to flower. These elongate slightly later than the principal flowering tillers and are not removed at the earlier cuts and so survive to flower later. Flowering at closer spacings appears to be more uniform, and more of the reproductive tillers are removed in the earlier cuts.

(4) Yields per sq. ft. tended to be higher at closer spacings as a complete ground cover was not achieved when the plants were wide apart. However, the highest yields were normally obtained from the 4″ spacings and not from the 2″, particularly if the plots had received nitrochalk, as even when the tiller numbers were lower (as they were until July in the 4″ spacing) the tiller weights were higher. The tendency over the two years was for yields at different densities to level up, the remaining discrepancies in tiller number being balanced by differences in tiller weight in the same way.

(5) The level of nitrogen does not affect the main seasonal trends, but high nitrogen raises the level of herbage production over the entire season. As it seems unlikely that nitrogen directly influences the process of photosynthesis the alternative is to suppose that a greater proportion of the products of photosynthesis must be utilised in the formation of top growth. This idea receives some support from the work of Sprague and Sullivan (1950), who showed that in cocksfoot the application of nitrate could stimulate the use of fructosan reserves for the production of shoot material. Evidence recently obtained by Vose (unpublished) also indicated that ryegrass grown at a higher nutritional level has higher shoot/root ratios and lower root weights. However, it should be borne in mind that lower root weights may not always occur, as stimulation of top growth would lead to a more rapid attainment of optimum light interception which might (up to that point) increase photosynthetic profits as a whole.

The aspect of growth most strongly affected by nitrogen is tillering. This has been demonstrated previously by Cooper (1951), who at the same time showed that leaf appearance on the main stem was not affected so much. The present results confirm that rate of tillering is influenced by nitrogen and ceases when the supply becomes inadequate.

The form of the production curves discussed here may be interpreted to a very large extent in terms of interception of available light energy and of the utilisation and distribution of the products of photosynthesis, as affected by the extent of reproductive growth and the level of soil fertility. Growth is particularly dependent on the

supply of nitrogen which ceases to affect it only when tillering is at a maximum or the sward becomes too dark for tillering to continue. Natural increases in light intensity will influence growth most when there is sufficient nitrogen to support fairly rapid tillering. If tillering ceases it seems unlikely that effective growth can continue for long.

Taking the results as a whole it seems that competition at close spacings was primarily for nitrogen and other nutrients. The available chemical analyses by Dr. ap Griffith show that when fertility was high nitrates accumulated in appreciable amounts at the 12″ spacing but not at the 2″, and it is considered that this indicates nitrogen was surplus to requirements only at the 12″ spacing.

It seems unlikely that competition for light is very materially affected by spacing, as the measurements made so far indicate that it is just as dark at the base of a spaced plant as it is in the sward.

The development of competition for light is illustrated in Fig. 2. Three leaves only are shown on each tiller as it has been observed at several different times of the year that tillers of S.24 carry an average of three leaves each at all spacings and nitrogen levels. In order to simplify Fig. 2, the leaf area indices are shown at about half the value which would be observed in practice.

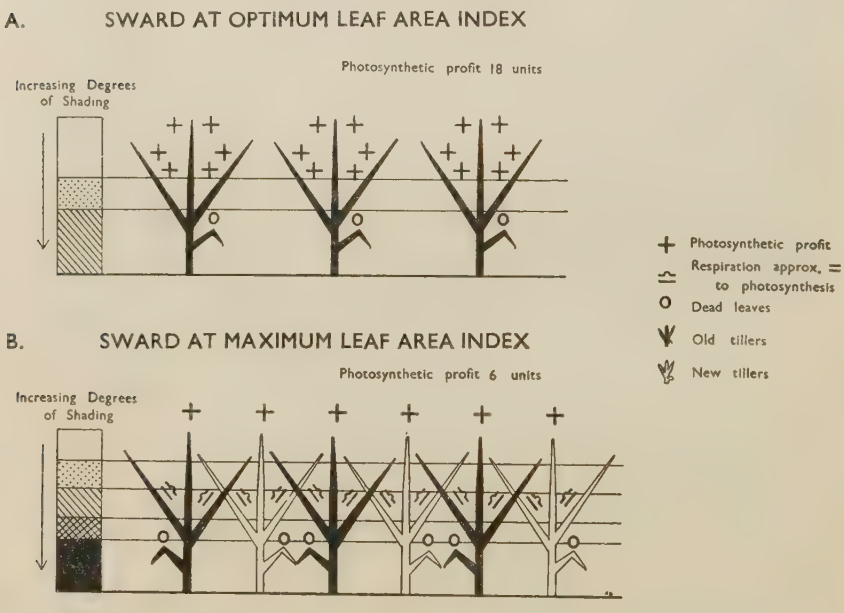

Fig. 2

(A) shows diagrammatically a sward which has just reached the point of maximum light interception. At this point photosynthetic profits are at their highest in relation to metabolic debits and the leaf area index is optimal. (B) shows a sward at the maximum leaf area index. The density has been increased by the utilisation of reserve substances to form new tillers, and light has been cut off from the lower leaves in such a way that the whole sward has been reduced to a point at which photosynthetic profits are very small.

This picture of the situation has several interesting implications. In selecting for productivity it is evident that a variety capable of rapid attainment of maximum light interception would be at an advantage in the first phase. This would depend not only on the rate of increase of leaf area (whether by more rapid appearance of initial leaves, a higher rate of tillering or larger leaf size) but would also be achieved more quickly at a flatter leaf angle.

Once maximum interception is established, however, the problem is that of maintaining effective growth for as long as possible on a fixed quantity of available light. As shading round the base of the plant inhibits tillering (Mitchell and Coles, 1955) the ability to continue tillering and to maintain numbers in conditions of shade is important. The maximum number of tillers needed will be less, however, if the leaves are larger. It is also probable that an increasingly steep leaf angle would facilitate the formation of a dense sward by enabling the maximum number of leaves to be placed so as to obtain adequate light for survival.

In practice, as tillering is likely to come to a halt on many occasions, a sward will tend to a large extent to become dependent on the growth, and in particular the size, of leaves on the individual tillers. Not only are most close swards short of nitrogen but nitrogen applications in the form of heavy block dressings are unlikely to lead to permanent increases in tiller numbers. It should also be emphasised that under frequent cutting a plant would spend a large proportion of its working life in the vegetative condition and this would in turn tend to lead to the maintenance of more or less stable tiller numbers from cut to cut.

Natural selection has probably favoured plants which carried substantial reserves in roots and stubble and were thus able to survive occasional periods of extreme frost or drought. However, in a temperate climate nitrogen can be applied fairly freely and reasonably heavy defoliations carried out without apparent detriment. It seems therefore that the products of photosynthesis should be used as far as possible to form leaf tissue. Some selection

work on these lines is in progress at the Station at present, but the selection techniques must be related to proposed management practices.

To a large extent therefore progress in breeding must be associated with the ability to produce at the required time the greatest bulk of herbage from the light available.

The most efficient system of management should lead not only to the best utilisation of light energy but also to the most satisfactory use of plant reserves. In practice these considerations must also be equated with the requirements of the grazing animal at any time and its ability to utilise the herbage on offer. An understanding of each component in the situation must be acquired if progress in grass breeding and agronomic practice is to be maintained.

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